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V. Depuis

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POST NATAL DEVELOPMENT OF THE GREY SEAL

A STUDY OF THE SUCKLING PERIOD, THE STARVATION PERIOD AND ENERGY UTILIZATION IN THE GREY SEAL (HALICHOERUS GRYPUS) DURING THE INITIAL MONTHS OF LIFE

BY

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-- FOREWORD --

The present study has been executed as a cand. philol. dissertation (MsC thesis) under the supervision of Professor John Krog, PhD.

The field seasons have been October 1978 in the Vega sector, and October 1979 in the Halten-Froan sector. Metabolic measurements were carried out at The Seal Laboratory, University of Oslo between May to September 1979. Costs of the undertaking were covered by The Zoophysiological Institute, and support from the Seal Fund for seal quarter and the field season of 1979 is acknowledged with thanks.

I wish to take the opportunity to thank Professor John Krog for his excellent, valuable supervision. Dr. Nils Are Øritsland has read through the manuscript during its preparation as well as providing guidance in APL-data system processing. Arvid Påsche, of Nutek, has also perused the manuscript. Appreciation is also expressed to Øritsland and Påsche for their excellent advice and interest.

The Marine Mammal Division of the Bergen Oceanographic Institute has been of great assistance in the field portion of the project. I wish to thank Torger Øritsland, Bjørn Bergflødt, Arne Bjørge and Kjell Arne

Fagerheim for their interest and kindness they have shown, as well as their excellent cooperation.

Tor Samulsen, of the Bergen Aquarium, was kind enough to make young seals and localities available for this study. Jeg would like to thank him, and the other staff, for their interest and good cooperation.

Scientific officer Age Jonsgård, of the Marine Biological Institute and Consultant Ernst Aas, of The Department of Fisheries gave me the opportunity to study seal in the fishing grounds in Vesterisen in 1979. Laboratory technician Morten Bronndal has always been willing to make a contribution with seal, both at Blindern and in the field. Without his experience and advice, it would have been difficult to complete this assignment.

The staff of the workshop division have always been congenial and have made a good job of building and constructing equipment.

University lecturer Else Sandved has provided statistical guidance.

I would also like to thank the other staff at the institute for the excellent professional atmosphere. Geir Taugbøl and PÅl Presterud, in particular, have contributed to this.

Warm appreciation is due the above mentioned persons and those who have not been mentioned, who have contributed help with this assignment.

Blindern, July 1982

Vidar Depuis

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INTRODUCTION

The grey seal, (Halichoerus grypus), is found in both the East and West Atlantic ocean areas (fig. 1.1). The population in the Baltic Sea and St. Lawrence give birth in February - March, whilst the British and associated populations have their deliveries from September - December (King 1964). For Norwegian grey seal, the birthing period is from the end of September to November.

The geographic location of the Norwegian grey seal areas in relation to the English is such that exchange of individuals between the populations can occur. It is therefore reasonable to

suppose that the Norwegian and the English grey seal populations do not differ essentially from one another genetically. Tagging experiments have shown that recapture of 8 - 10 week old grey seals from England is not unusual along the Norwegian coast (Hickling et al.1962). Adult English grey seal were not reported at this point in time, but the article indicates that this was a possibility. In another article on seal along the Norwegian coast (Øynes 1964), the author writes that the stock of grey seal in Halten-Froan sector must have increased markedly after 1956. He proposed that an immigration from England could be a possible cause for this.

A study of the Norwegian grey seal pups' suckling period could therefore, combined with studies of grey seal pups' suckling period in England (Coulson 1960, Bonner 1972), provides interesting information. Comparison of the diurnal weight increase, the suckling period's duration and the mortality of Norwegian and English grey seal pups is especially interesting. It is known, from human studies, that there has been an increase in growth and total height in fully grown adults, this being concomitant with an improvement in nutrition (Liestøl 1980). It is reasonable to presume that the same is true of other mammals. When seals living on a nutritionally minimal level have pups, one would expect that the condition of the mother would have consequences affecting weight increase in the pups during the suckling period. When the growth rate in such young is compared with the growth rate in young from seal populations living under nutritionally more favourable conditions, one would expect to find a

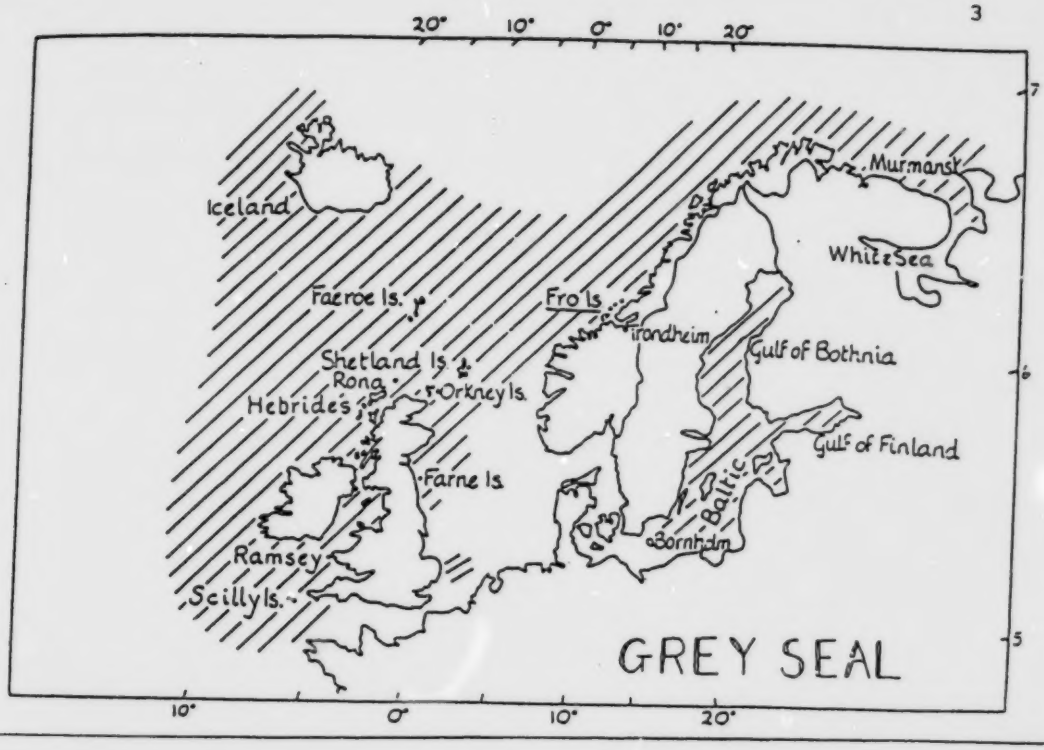
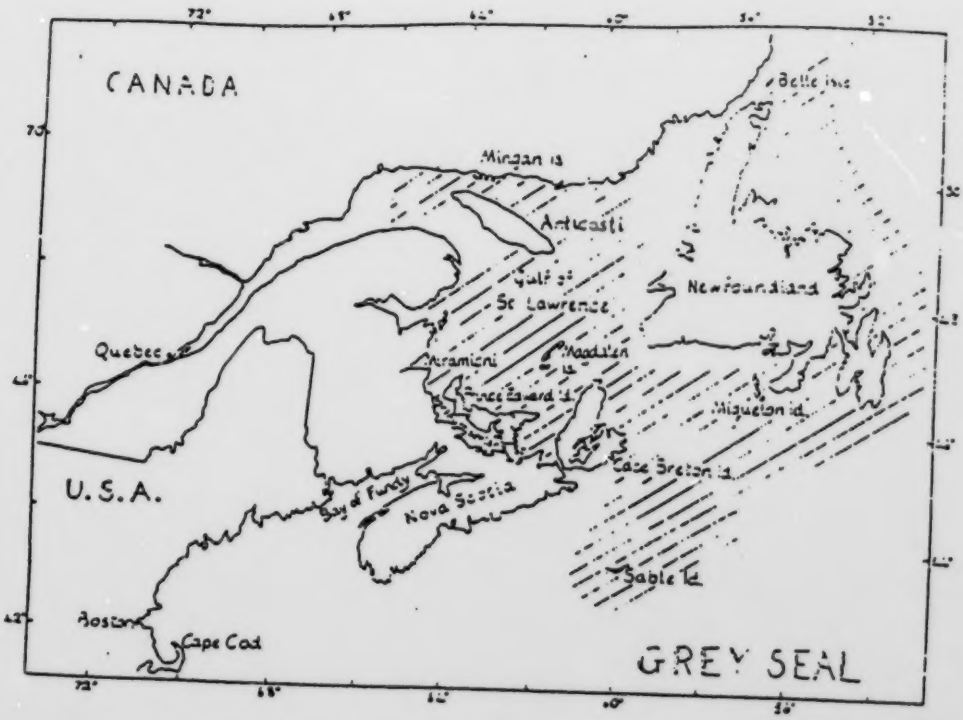


Fig. 1.1 Distribution of Grey Seal (Halichoerus grypus) in the East and West Atlantic Ocean

(King 1964)



somewhat lower rate of growth in the first mentioned. Over time, the size of the individuals in a nutritionally ill-favoured population becomes less than that of individuals in a nutritionally favoured population. There is also reason to believe that smaller animals will be poorer milk producers than larger animals. Mansfield (1977) established that the Canadian grey seal was larger and heavier than the English. Weight increase in the Canadian grey seal pups during the suckling period was also somewhat greater compared with that of English grey seal pups; 2.1 kg/24 hours against 1.8 kg/24 hours. In addition, the suckling period for the Canadian baby seals was 14 - 15 days, whilst the English seal pups had suckling periods of 16 - 21 days. The comparisons made by Mansfield (1977) are based on data from Bonner (1972) and Coulson (1960).

Information on the Norwegian grey seal can thus contribute by illuminating problems pertaining to discussion on whether the English grey seal has exceeded its natural resources, since the Norwegian grey seal population, in all likelihood, is genetically closest to the English grey seal population.

The largest population of grey seal along the Norwegian coast is found in the Halten-Froan sector in South Trøndelag. The seal pups here have a suckling period of two - three weeks, followed by a period of starvation (King 1964). The duration of the starvation period is little known, but recaptures of seal pups in nets suggest that these have eaten little or nothing for a period of six - eight weeks following weaning. An eight week old seal pup not weighing more than 15 kg was reported, but a weight of 25 kg is more usual for

seal pups of the same age (Hickling et al., 1962). The pups' weight during the starvation period will depend upon time, weight on termination of suckling and activity during the starvation period.

The grey seal pups are born with a relatively long-haired yellow-white fur coat (lanugo fur or whitecoat), and the blubber layer at birth is not more than 0.5 - 1 cm thick. It has been demonstrated that Greenland seal pups have brown fat at their disposal for "non-shivering thermogenesis" for the first two - three days after birth (Blix and Steen 1979). It is reasonable to assume that this holds true for other species of seal. When the brown fat is used up, the seal pups will have to rely on having sufficient subcutaneous insulation to be able to maintain deep body temperature under all circumstances. Newborn grey seal pups are, strictly speaking, adapted for dry cold. This means that they have good insulation when the fur is dry. Wet fur, on the other hand, is a poor insulator if it cannot trap air between the hairs. Whitecoat fur, when wet, pastes itself to the skin, and this fur holds little or no air in water (personal observation).

Measurements of blubber from seal and hides, including those from polar bear and reindeer, showed that the fur's insulating capability in air is more than double that of blubber of the same thickness. In water, fur is a relatively poor insulator (Scholander et al. 1950 a). The water in the fur will, however, be little replaced in the proximity of the skin. This stagnant water layer will therefore reduce heat loss from the fur-covered skin compared with

hairless skin (Frisch et al. 1974).

In an study of dead and living blubber, it appeared that the insulating capacity of living blubber in the common seal (Phoca vitulina) was 50% of the corresponding thickness of dead blubber. The conductivity for living blubber was 2.5 cal/cm/°C (Hart and Irving 1959).

Corresponding studies on whale showed that living blubber had a heat efficiency that was 30% higher than the heat efficiency of dead blubber of similar thickness (Kanwisher and Sundnes 1965, 1966). The conclusion of these findings seems to be that blubber as insulation material is highly dependent on the blood flow in this tissue.

To obtain wet cold insulation (blubber) as quickly as possible, it is important that the milk the baby seal drinks is rich in nutrition. That is to say that it contains plenty of fat. In one study, it was found that the milk contains as much as 52.3% fat (table 1.1). Table 1.1 shows the composition of milk in a number of animals. It demonstrates that there is a recurrence of high milk fat content in in marine mammals.

Table 1.1

Milk composition in several marine mammals, polar bears and cows

Species	Water	S.m.	Fat	Prot.	Lact.	Ref.
Blue whale	47.2	52.8	38.1	12.8	---	1
Hooded Seal	49.8	50.2	40.4	6.7	---	2
Grey seal	32.3	67.7	53.2	11.2	2.6	3
Polar bear	55.9	44.1	31.1	10.2	0.5	4
Cows	87.5	12.7	3.7	3.5	4.8	5

The figures are expressed in percentages. S.m. means solid matter, Prot. means protein, Lact. means lactose. The table does not include ash.

1 Miller Ben Shaul 1962

2 Sivertsen 1941

3 Amoroso and Mathews 1951

4 Baker et al. 1963

5 Spector 1956

In addition to the fact that seal milk has to be highly nutritive, the mother has to render it concentrated so as to avoid losing too much water. Even if studies show that some seals and fur seals can drink salt water (Gentry 1981), one knows little about how seals regulate their water balance. Drinking of salt water has been observed in true seals during seal hunt (Brown 1952, Harrison and King 1965). Whether such cases represent actual drinking or merely apparent, is difficult to determine (personal observation).

Big changes in body weight and body composition occur in the course of a grey seal pup's suckling period. The fur coat alters as well during this time, finally changing from the fine whitecoat to adult seal fur. The weight gain is due primarily to an increase in the blubber layer, and to a somewhat lesser degree to growth. In Coulson's work (1960), it was stated that the birth weight for grey seal pup was 14 kg for females and 14.5 kg for males. There was also a corresponding difference in daily weight gain; 1.7 kg for females and 1.9 kg for males. The author reported the suckling period to be 17 - 18 days. He found that length and circumference increase by 21% and 56% respectively during the same period. In cm, this corresponds to an increase in circumference of 60 - 95 cm. In length, it is equivalent to an increase of 90 - 110 cm (the figures have been rounded off).

In an study done ten years earlier, Davies (1949) estimated the suckling period to be 15 - 17 days. Other English studies have estimated 18 and 16 - 21 suckling-days (Amoroso and

Mathews 1952, Bonner 1972). Mansfield (1977) declared birth weight in Canadian grey seal pups to be 17 kg. The average length increased from 86 to 106 cm and the circumference increased, on average, from 65 to 101 cm in the course of the suckling period - an increase of 22% and 55% respectively. The author found, moreover, that the weight of skin and blubber in the young increased by 4 - 23 kg during the suckling phase and the weight increase for the rest of the body was, on average, 13 - 23 kg. On termination of suckling, a Canadian seal had an average weight of 46 kg.

By considering the pup to be a cylinder and looking at volume changes, Coulson estimated that it increased its volume 2.8 times in the course of the suckling period. The increase in diameter accounted for 76%, the increase in length 24% of the volume expansion. On the basis of density characteristics and growth in length, which the author reckoned as real growth, he estimated that 50% of the weight at the termination of suckling was blubber. This agreed with Mansfield's (1977) estimates.

Mansfield (1977) found that the relation between the mother's weight loss and the pup's weight gain during the suckling period in the Canadian grey seals, was almost identical to the corresponding case found by Amoroso and Mathews (1951) in captive grey seal. This comprised a loss of 43.0 kg in the seal mother, from 168 to 125 kg and a gain of 19.5 to 41.7 kg in the pup's weight. The determinations were carried out from three days after birth. Mansfield found, furthermore, that 60% of the mother's weight loss derived from blubber and 40% from the rest of her body. The ratio

between the mother's weight loss and the pup 's weight gain corresponds to 1:0.5.

Following the suckling period, the grey seal pups have a starvation period lasting several weeks (Hickling et al. 1962). The diurnal weight loss during this period was measured as 0.5 kg (Coulson 1960, Mansfield 1977). Mansfield found that the weight of carcass and skin, including blubber, maintained a 1:1 ratio in the post-weaning period. A study of Greenland seal pups (Pagophilus groenlandicus), concluded that 10% of the weight loss during the starvation period derived from blubber, and 35% was reduction in carcass weight (Stewart and Lavigne 1980).

The composition of nutrients consumed during starvation is evident from the ratio between O_2 uptake and CO_2 production, RQ (Respiratory Quotient). Oxygen uptake and weight decrease will be a measure of how much a kg of weight loss corresponds to in energy equivalents. A comparative field measurement, and metabolic studies in the seal laboratory, will provide data that will elucidate which nutrients are consumed and the amount of these in the seal pup's starvation period.

Deep body temperature in mammals is held within relatively narrow limits. Too high a temperature leads to denaturation of protein and heat death, while low temperatur results in reduced ion permeability, and in consequence slower nerve conduction, as well as lower reaction rates for chemical reactions in the body generally. Factors governing heat balance are thus vital for

the individual. Insulation, conduction, convection, radiation, evaporation and metabolism are the most important of these factors. The metabolism will provide heat, while, for example, evaporation will result in heat loss. In water, the skin temperature in seals will normally lie 1.0 °C over the temperature of the water. This means that the heat radiation from the seal's skin remains minimal. In air, the skin temperature will be higher in relation to the ambient temperature, and radiation will be of greater significance (Irving and Hart 1957). Radiation works both ways, however, and can also promote warming (Øritsland and Ronald 1973, 1978).

The ratio between metabolism and body temperature in homeothermal animals can be summarized in a modified form of "Newton's law of cooling (Scholander et al. 1950 b).

$$T_r - T_c = I_s \cdot M$$

T_r = core body temperature.

T_c = critical temperature.

I_s = maximal insulation for the entire body.

M = the animal's metabolism (heat produced).

Lower critical temperature is the lowest temperature the environment can have without the animal's metabolism rising.

Despite the counter-current arrangement in flippers and active regulation of heat emission through the blubber, sea mammals have long been known to have a high resting metabolism (Irving et al. 1936, Scholander 1940).

Measurements in the studies mentioned have been performed on young animals, that generally have a higher resting metabolism than adult animals. The results in these undertakings must therefore be presumed to be influenced by this fact. A newborn common seal has, for example, a resting metabolism that is 3.5 times higher than that of an adult individual. For a common seal pup of 3 - 5 months, the metabolism lies 2.2 times above the resting metabolism of an adult individual. Computations are performed on the basis of oxygen uptake in ml per g per hour (Miller and Irving 1975, Matsuura and Whittow 1973). Miller and Irving wrote that no account was taken in the calculation of the proportion of fat-free body weight. They were of the opinion that the difference in the metabolic rate in young animals as relation to adult animals , would then have been much less. Oxygen uptake was:

Adult common seal	0.23 ml O_2 /g/hour
3 - 5 mth common seal	0.5 ml O_2 /g/hour
1 mth common seal	0.8 ml O_2 /g/hour

In Kanwishers and Sundnes' (1965) publication on porpoise, the authors claim that the latter can only maintain normal high body temperature through a combination of high metabolism and appropriate insulation with the aid of blubber. They proposed that the porpoise (or the seal) is the aquatic equivalent of the shrew (Sorex cinerus). The latter has also a much higher resting metabolism than could be expected from computations made on the basis of weight (Morrison et

al. 1959). The authors attempted to explain the high metabolism on nutritional grounds, something Kanwisher and Sundnes (1965) found speculative. In any case, the shrew does not follow the usual Kleiber rule that $M = 70.W^{0.75}$, where M corresponds to Kcal per 24 hour day and W is the mammal's weight in kg (Kleiber 1975).

In work by Kanwisher and Sundnes (1965), it has been proposed that it was the thermal barrier that limits the downward size of the shrew. Water has a specific heat capacity around 3000 times greater than air per volume unit. The conductivity of water is, moreover, almost 25 times greater than the conductivity of air (Weast 1975). This illustrates the problem young sea mammals must have with heat equilibrium; at the same time they are highly interesting from a comparative thermoregulatory point of view.

In the present study, it was natural to take up a few viewpoints relating to food supply and thickness of the blubber layer. In an article on population increase, the authors assert that a seal population that increases in number, will sooner or later arrive at a situation when prey per capita is reduced as a result of intraspecific competition. The consequences of this are either that the blubber layer is reduced as a result of lower food intake, or that it is preserved. In order to avoid consuming the blubber layer, the seals have to be more active than previously, because the seals have become more numerous and the density of prey animals less. Preservation of the blubber layer therefore demands, indirectly, more energy than before. If the blubber layer is reduced and becomes thinner than 2 - 1.5 cm, the thermoregulatory conditions will deteriorate, such

that the seal is obliged to utilize more energy in order to maintain the heat equilibrium (Brodie and Påsche 1980). The authors claim that large seal herds will require proportionately more energy than smaller (assuming that there is more competition for food in the larger population than the smaller). In their study, they see no reason to suppose that a large seal herd will utilize the energy more efficiently, as is claimed in two articles that they cite (Winters 1975. Innes et al. 1979).

Brodie and Påsche (1980) built their article on measurements of oxygen uptake by grey seal pups during the starvation period, together with reduction in weight and measurements of the blubber layer during this stage. They measured resting metabolism in the animals. Out in the open, the seals are active for a great part of the twenty four hour day. It would therefore be interesting to look at the energy consumption in a lean, poorly insulated seal in comparison with a seal equipped with a normally thick, well-insulating blubber layer. When seals swim in cold water, it can happen, for example, that a lean seal has to use appreciably more energy than a seal with a normally thick blubber layer, because heat loss by convection will rise. Metabolic studies during activity and at rest in water for a lean and normal seal (with ordinary blubber layer) will provide information on this point.

The follow study is aimed at determining seal pups' weight gain during the suckling period, and the weight loss in the subsequent starvation period. The study will be carried out on pups born in the

Halten-Froan sector. This will then be compared with metabolic studies, carried out in the Seal Laboratory at Blindern, in order to account more closely for their energy requirements during the initial months after birth. A comparison of weight gain in English and Norwegian grey seal pups during the suckling period is interesting from an ecological point of view, since that can give clues as to the condition of the stock related to the living conditions and the food supply in a dense and less dense population.

Approach to the problem:

1) How does the weight of grey seal pups in the Halten-Froen sector increase during the suckling period?
2) What is the course of events relating to weight loss in these seal pups following termination of suckling?
3) How does energy utilization vary with varying water temperature in a lean, and well insulated seal, at rest and in active state during free dives?

MATERIAL AND METHODS

Field Experiments:

These were carried out in collaboration with the Directorate of Fisheries' Marine Research Institute, Marine Mammal Division, Bergen. The work consisted of visiting those islets and rocks where seal pups were present, go ashore on these spots and tag and weigh the pups. To get to and from the seal areas, and not least when landing, a rubber dinghy was necessary. Tagging was performed with nylon tags in the back flippers (fig. 2.1). The weighing was carried out by putting the seal pup into a bag and hoisting it up a scale (fig. 2.2). The scale was of the Sauter 0 - 100 kg type, accuracy ± 0,1 kg. The seal pup's weight could vary somewhat due to the fur being dry or wet, maximum ± 1 kg. Attempts were made to even this out by whenever possible.

In the autumn of 1978, the circumference and length of the seal pups in the Vega sector were measured. In 1980 and 1981, corresponding measumments were made on seal pups in the Bergen aquarium. It is difficult to keep seal pups still during such measurements, and this fact introduced a considerable measure of uncertainty. In the studies on seal pups in the Halten-Froan sector, it was therefore decided to focus on weight gain during the suckling period. A depiction of circumference and length measurement is given in fig. 2.3.

Measurement of blubber thickness in living grey seal pups would also have been interesting. An ultra sound apparatus was

available for this purpose, but owing to the risk of and the effect of sea spray on the apparatus, it was not employed during the field experiments.

Length and circumference measurements:

Measurement of length was carried out on two or more, by placing the measuring tape along the seal's back and reckoning from the snout to the tip of the tail. It was hard to keep the animals still during the measuring process which was therefore time-consuming and fraught with great uncertainty. This was particularly the case where estimation of length was concerned, by reason of the seal's flexible neck (King 1964).

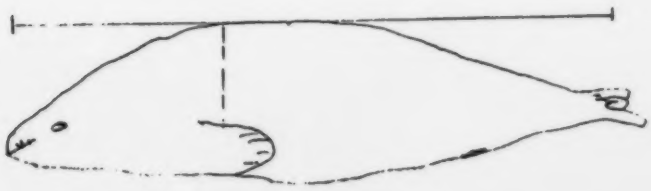


Figure 2.3 demonstrates how length and circumference of the seal pup are determined

Figure 2.1
shows tagging of
a grey seal pup.

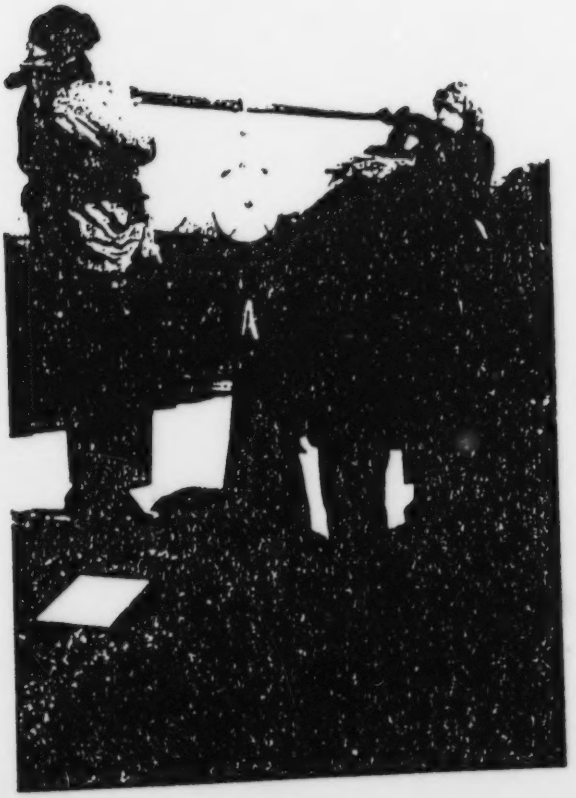


Figure 2.2
shows weighing
of a grey seal pup.

Age Determination:

The appearance of the umbilical cord is the most reliable distinguishing characteristic to use in age determination of grey seal pups. The umbilical cord is lost when they are 4 - 5 days old (personal observation Bergen 1979, Hewer 1957, Hickling 1960, Davies 1949). Age was determined in three pups by the fact that they were losing their umbilical cord.

The seal pup's behavior was mentioned i connection with age determination. Before the pups are two days old, they exhibit comparatively little aggression, but after this they become more "hot-tempered". At the same time, there is a dividing between poor and good motor functioning at two days old. (Hewer 1957).

Dentition varies with age in grey seal pups (Telfer and Watt 1953). That was also confirmed in this study. Age determination on the basis of dental development was therefore not used. Telfer and Watt stated also that they had utilized moulting to determine age in the seal pups. In the Halten-Froan sector, it was found, however, that moulting in seal pups showed considerable individual variation. Age determination based on moulting was therefore uncertain.

As an example one could mention a seal pup that was thought to be two days old at most, with black head, black claws and a pink umbilical cord. Two days later, it was found again, and its umbilical cord still intact. The colour of the claws is also used in determinating age (Hewer 1957), but not even this can be used with confidence. Claw colour should be white until the seal pup is about four days old (Hewer 1957, Hickling 1960). // Observations in the area

can provide information on whether seal pups are newborn or not. By regularly checking islands and rocks, one will discover any possible pups that have been born since the previous time one was there. If this period is short and the seal pup satisfies the new born physical criteria (table 2.1), they are recorded as newborn.

The age of some seal pups can be determined by the finding of fresh blood on the rocks or in the seal pup's coat, or in both places. Those criteria that were utilized in age determination in this study are noted in table 2.1.

Table 2.1 Criteria used in Age Determination of Grey Seal Pups in the Halten-Froan sector.

Age in days	Criteria
0 - 4	All the seal pups have intact umbilical cord
0 - 2	Poor motor function, little aggression
2 - 4	Better motor function, is aggressive
0 - 1	Fresh blood on the rock or in coat.
	Observations that they were not there on previous day

The criteria for the three first groups in the table are from Hewar (1957).

The seal pups' motor function and behavior have been mentioned earlier to be unreliable criteria. It might be appropriate to cite one example. One day, a seal pup came swimming towards the rubber dinghy after being called. It was not aggressive, swam well, had a pink umbilical cord and weighed 14.5 kg. It was obviously

newborn.

After the suckling period, the seal pups will lose weight. To estimate this weight loss, the seal pups ought to have been continuously monitored so that it could be established that the seal pup had not been nursed during the period surveyed. The area extends over many square kilometers, and such monitoring would have been impossible. Seal pups in whom weight loss has been noted several times, will, however, provide trustworthy data; it is not reported that seal mothers terminate suckling only to start it again after a break of many days.

Laboratory Experiments:

Experimental Animals

Four grey seals (Halichoerus grypus), caught in the area west of Vega were employed in the experiments. Three of these, two females and one male were caught in October 1977. The youngest, a female was caught in October 1978. During the experimental period, which lasted from May to September 1979, the animals were held in the seal laboratory at the University of Oslo, Blindern. The three oldest were somewhat thinner, but seemed otherwise alert and healthy. The youngest seal was in good condition. Weight, circumference, length and blubber thickness are given in table 2.2.

Table 2.2

Age is given in months, weight is given in kg, length, circumference and blubber thickness are given in cm. Weighing and measurement on 6 June, 1979

Age	Sex	Weight	Blubber	Length	Circumference	No.
20	female	41.5	1.5	128	88	1
20	female	49.2	1.5	130	92	2
20	male	59.0	1.5	146	99	3
8	female	51.2	3.0	121	95	596
Weighing and measuring as of 22 August, 1979						
10	female	55.0	3.5	131	100	596
22	female	49.0	3.0	-	-	1

In the seal laboratory at Blindern, fresh water is employed in the tanks. Salt tablets are therefore added to the feed, which consisted of whole frozen herring. In order to compensate for any deterioration of feed with freezing, vitamins and minerals were added.

The Blubber Measurements:

The problems involved in keeping the animals still during the measuring of length and curcumference have been mentioned. The same was true when estimating blubber. The method here consisted of one person sitting on the back of the seal and holding its front flippers and head fast, after which the blubber thickness was estimated on the sides of the hind part of the seal's body. Here, a

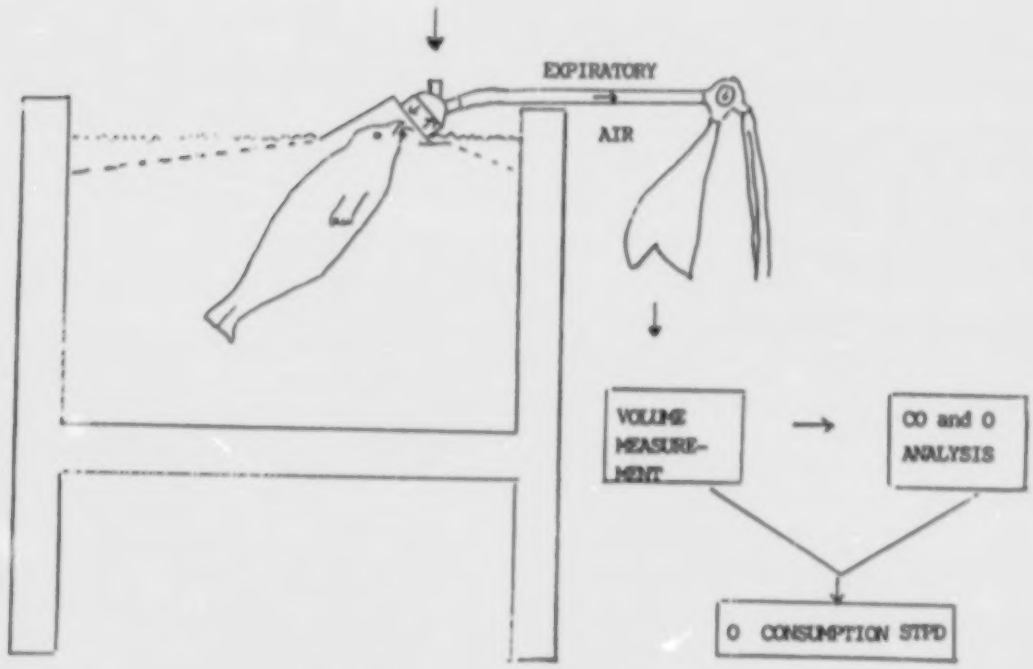
saline cream was rubbed in to facilitate contact between the seal skin and a probe connected to the ultrasound apparatus. The apparatus was of the type Kretz Technik, Impulse Echogäret = = 24 me. Accuracy within the measurement range was stated as ± 10%. This apparatus was equipped with an oscilloscope with a cm scale, where the blubber thickness appeared as a peak on an otherwise even graph. There often appeared several such peaks, for example at 4,8 and 16 cm, due to reflections. In these cases, it was useful to check blubber thickness by taking a skinfold between the fingers, so that the correct value was used. The skinfold method was not better than the ultrasound method, but it was possible to judge whether the blubber thickness lay nearer two than four cm (the screen reading divided by two). The apparatus was also very sensitive to movement, so that the measuring process in these cases could be very protracted.

Metabolic Measurements:

The experiments were carried out in a round tank, three metres in diameter and 1.4 metres deep. The oxygen uptake was measured during activity and at rest (repose) at different water temperatures.

Oxygen uptake was measured by utilizing the breathing hole technique (Påsche 1974). This technique is a variant of ordinary open spirometry where a person breathes normal air through an oral/nasal mask, the expired air being collected in a Douglas bag (rubber bag) (fig. 2.4).

Figure 2.4 Oxygen uptake and Breathing Hole Technique



In the breathing hold technique the mouth/nose mask is replaced by a respiration bell of plexiglass equipped with one-way valves (fig. 2.5). The respiration bell sits in a net that is stretched securely about ten cm below the water surface in the experimental tank (fig. 2.4). The interior of the respiration bell is so shaped that the seal's snout can approach close to the two one-way valves, in such a way that the expiratory air goes directly out into the expiratory valve. This eliminates the possibility that CO_2 gas will dissolve in water instead of being collected in the Douglas bag. The expiratory valve is connected to a four metre long flexible hose, with a one-way valve at the end. Inside diameter of the one-way valves is about 3 cm, and very little opening pressure is required. Respiration is therefore impeded only to a very slight degree by peripheral resistance in the gas collecting system, provided that the respiratory tube is regularly emptied of condensation water.

The tube from the respiration bell is coupled to a three-way cock. The expiratory gas is collected continuously in Douglas bags by altering the outflow by means of the three-way tap. The collecting periods lasted from ten to fifteen minutes. After a Douglas bag was filled, the three-way cock was turned so that a new bag could be filled while sampling was going on. The gas in the full bag was mixed well. The test samples for gas analysis were withdrawn into 50 ml glass syringes, equipped with airtight cocks that could be opened when needed. During sampling from the bags, the gas was drawn in and out two - three times to ensure that the residual gas in the syringes was flushed out. The syringes were placed on a rack for

later analysis. The gas volume in the Douglas bag was measured with a previously calibrated wet gas meter (producer Nordgas a/s). Prior to the experiments, the syringes were smeared with silicone grease, the gas collecting system tested for leakage and the O_2 and CO_2 analysers warmed up for at least an hour. These were calibrated before every series with gas analysers.

Fig. 2.4 a

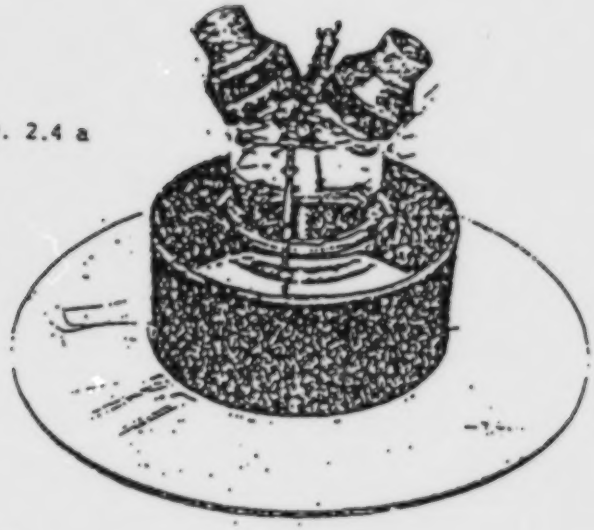
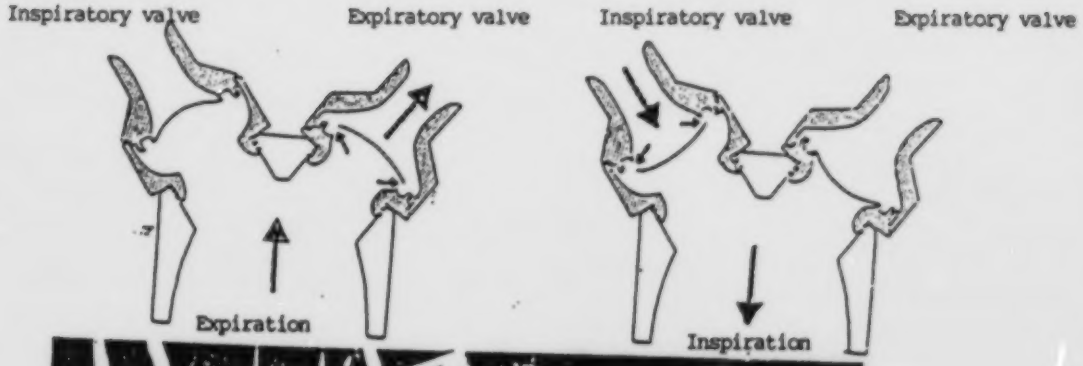


Fig. 2.4 b



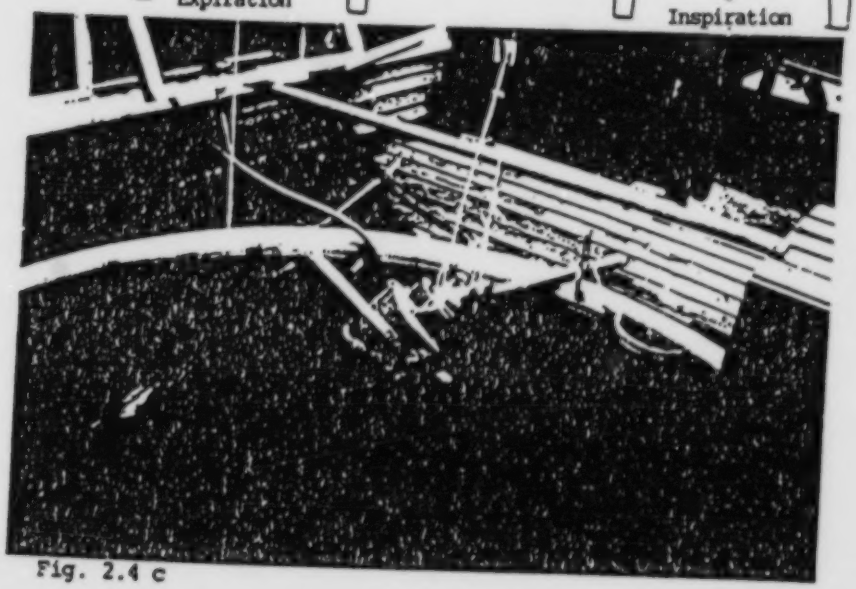


Fig. 2.4 c

Figure 2.4 a. Respiratory bell with one-way valve. 2.4 b. Method of operation of the one-way valves (The figures taken from Pasche 1974). 2.4 c Shows the experimental lay-out in practice.

After collecting four duplicate samples from four Douglas bags, the expiratory air was analysed for O_2 and CO_2 content. For this purpose, a Beckmann OM 11 and a Beckmann LB 2 were employed. The gas analysers were calibrated with exterior air and calibration gas saturated with water vapour. The paired composition in the calibration gas was 11.88 volumes per cent O_2 and 4.85 volumes per cent CO_2. The calibration gas was previously calibrated using a Scholander ½ cc gas analysis apparatus (Scholander 1947). The Beckmann analysers were stable for a ten minute period following calibration. The stated margin of error for the O_2 analyser was given as 1.0%, the CO_2 analyser had a margin of error of 0.75%. The wet gas meter 's margin of error was 3%.

The highest value for CO_2 and the lowest value for O_2 gas was consistently employed, when the CO_2 content in the syringes could not increase, and O_2 content in the syringes could not decrease while they stood in the rack. By employing many duplicates in every series, the leakage could be eliminated more easily. Before every test series, readings were taken of outdoor temperature, indoor temperature, water temperature and barometer pressure. In protracted studies these values were checked at the end of the experiment.

The expiratory air never remained in the Douglas bags for longer than 10 minutes and the glass syringes were stored for a maximum of three hours, but usually for 50 minutes. It is known that gas composition in the Douglas bags changes with time; this occurs later in the case of glass syringes (Shephard 1955).

In order to check the seal's breathing periods in the respiration bell, a temperature-sensitive copper/constantan

thermoelement, coupled to a scriber, was inserted into it (Krog 1962). This checked whether the seal tried to breathe elsewhere by lifting up the net. When there were long intervals between breathing periods, the seal's behavior was checked.

The oxygen consumption was calculated using the formula

$$\dot{V}O_2 = \dot{V}_E \cdot \frac{FiO_2 - FeO_2 - FiO_2 \cdot FeCO_2}{1 - FiO_2}$$ (Brown 1973).

Feed intake is of significance when determining resting metabolism. The animal must be in a post-absorptive phase and in a thermoneutral environment (Kleiber 1975). During the experiments, the seals were fed in such a way that it took more than 12 hours from the last feeding to the start of the experiment. In this way, elevated metabolism due to digestion of nutriment, particularly proteins, will be avoided (Kleiber 1975).

In experiments where the water temperature deviated from the water temperature the seals usually swam in, they were allowed an acclimatization period of at least three hours.

During the experiments, resting metabolism and sleeping metabolism were deemed to be identical. There were no opportunities to measure brain activity using electroencephalography. For the purpose of the experiments, sleep is defined as having occurred when the seal is very calm and does not react to movements. Diurnal variations in the metabolic studies have been disregarded since the standard deviation in these measurements was far beyond that conceivably contributed by diurnal variations. The experiments were, nevertheless, on the whole, arranged in the afternoon , after

normal working hours.

Statistics:

The average values are computed as mean ($\bar{x}$) ±

Standard Deviation (S.D.)

The mean value is given by $\bar{x} = \frac{1}{n} \sum_{i=1}^{n} x_i$

Variance is given by $Var = \sum_{i=1}^{n} \frac{(x_i - \bar{x})}{n}$

S.D. is given by $S.D. = \sqrt{Var. \frac{n}{n-1}}$

Standard Error is given by $S.E. = \frac{S.D.}{\sqrt{n}}$

Regression analysis has been performed with a Hewlett-Packard 9815 A Calculator. This has a general statistics program that includes multiple regression analysis. Eight different types of graph were tried out, using the method of least squares. The best fitting graph, based on biological and statistical correlations, was chosen. The confidence interval was found by the approach given in Zar (1974).

In order to test whether two selections differ from one another, the two-tailed t-test is utilized. Use of the t-test assumes normal distribution or a large amount of material. To test whether more than two selections differ from each other , one-way grouped variance analysis is employed (Sverdrup 1973).

Signicance level is read off from statistical tables (Zar 1974) with the help of the calculated t-value or F-value. A level of 5% or less is reckoned to be statistically signigicant.

(Calculation of the seals' oxygen uptake was done on December 10 using APL system.)

3.1.1. WEIGHING OF GREY SEAL PUPS IN THE HALTEN-FROAN SECTOR IN THE AUTUMN OF 1979

During this field period, 90 seal pups were tagged and weighed. In all, 47 of these pups were re-weighed. Weighing started on 06.10.1979 and went on for a week. After that there was a pause of 11 days before the weighing was re-commenced. The latter weighings were done in order to obtain information on weight loss in the grey seal pups during the starvation period following the suckling period.

The pups' weight in the first period varied from 14.5 to 61 kg. Regression analysis on recorded weights and weighing dates during the initial period gave a correlation coefficient of 0.05, and the gradiant coefficient for an equivalent straight-line graph (diurnal weight gain) was not in accord with the measured results.

The weight of newborn seal pups was 16.6 ± 1.3 kg (S.D., n = 9). Age determination was carried out according to the criteria given in table 2.1. Four seal pups, about four days old, were also weighed. One of them was estimated to be nearer five days old, as the umbilical cord was almost lost. The results of weight measurement on age determined seal pups are expressed graphically in figure 3.1.1.1. In the same figure , the best-fit graph calculated by regression analysis is drawn. This graph was straight line ($Y = a + bX$). For age-determined seal pups, the weight-gain graph during the suckling period is: $Y = 16.6 + 1.9\ X$. The determination coefficient $R^2 = 0.97$. The 95% confidence interval of $b = 1.9 \pm 0.1$. Y is the

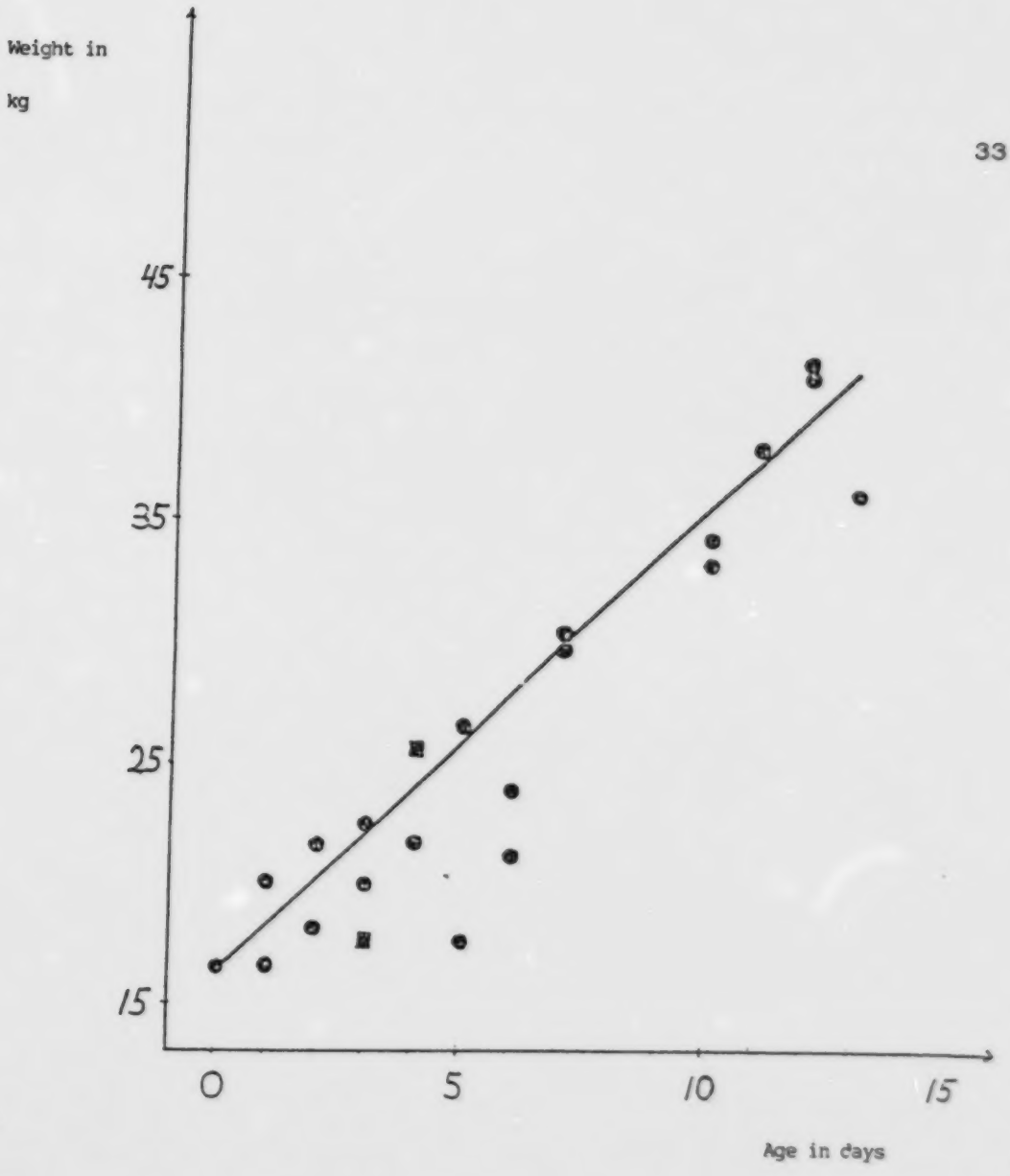


Figure 3.1.1.1. Weight gain in relation to age in age-determined seal pups, based upon characteristics given in table 2.1. Solid black circles signify one seal, solid black squares signify two seals.

seal pup's weight in kg, X represents age in days. The weight gain in seal pups of different sex during the suckling period showed no statistically significant difference ($p > 0.05$ with the two-tailed t-test). This was also the case when upper weights of all female and male seal pups weighed was compared.

By dividing up the seal pups according to mean weight of two successive weighings, and comparing the diurnal weight gain within the selected weight classes, it appeared that there was a statistically significant difference ($p < 0.05$) between the different weight classes, using variation analysis, one-way grouping. The weight classes were as follows: Group 1, seal pups that weighed less than 25 kg. Group 2, seal pups that weighed between 25 and 35 kg. Group 3, seal pups that weighed more than 35 kg. Drawing of lots was employed in the case of seals that could be placed in more than one group because they were weighed three times in the course of the suckling period).

Grouping according to weight class is entered in table 3.1.1.1, the average daily weight gain within each group is depicted in figure 3.1.1.2. Some seal pups were weighed three times in the course of the suckling period. The progress of weight gain in these seal pups is depicted in figure 3.1.1.3.

The average daily weight gain for all seal pups during the suckling period was: 2.10 ± 0.86 kg (S.D., n=28).

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Table 3.1.1.1. GROUPING OF SEAL PUPS ACCORDING TO WEIGHT DURING THE SUCKLING PERIOD, AND WEIGHT GAIN WITHIN EACH GROUP.

V1 is weight on first weighing, V2 is weight on second weighing. Dd is no. of suckling days, and V/d represents daily weight gain. All weights are given in kg. The seals are recorded by number and sex.

Nr.	D..	V1	V2	Dd	V/d
2704	♂	17.7	21.7	2	2.00
2708	♂	16.6	29.5	6	2.15
2712	♀	21.5	26.5	3	1.67
2717	♀	19.2	20.0	3	0.27
2724	♂	22.8	22.0	3	-0.27
2726	♀	17.5	24.0	3	2.17
2738	♀	17.0	20.0	2	1.50
2761	♀	16.5	17.5	2	0.50
"		17.5	21.0	1	3.50
2769	♂	18.0	17.5	1	-0.50
2793	♀	16.0	20.0	1	4.00
2825	♀	15.5	25.5	11	0.79

Group 1: Mean weight 20.5 ± 4.0 kg, V/d = 1.54 ± 0.65 kg (S.D., n = 9).

2706	♂	25.0	31.0	2	3.00
2709	♂	21.7	34.0	6	2.05
2711	♀	27.2	49.0	15	1.03
2713	♂	26.5	38.5	6	2.00
2722	♂	24.4	32.5	3	2.70
2723	♀	27.0	32.0	3	1.67
2730	♂	32.0	34.2	1	2.20
2732	♀	30.5	38.0	4	1.88
2734	♀	30.7	41.5	13	0.83
2741	♀	25.0	32.0	3	2.33
2756	♀	26.0	28.0	2	1.00
2765	♂	26.0	29.0	1	3.00
2795	♀	18.0	41.0	12	1.92
2796	♀	21.5	42.5	12	1.75

Group 2: Mean weight 29.8 ± 6.2 kg, V/d = 2.13 ± 0.58 kg (S.D., n = 12).

2701	♀	30.0	51.0	4	5.25
2703	♀	40.0	45.3	2	2.65
2731	♀	29.5	44.5	6	2.50
2733	♂	36.0	44.0	3	2.67
2736	♂	37.5	49.0	6	1.92
2744	♀	38.0	43.7	3	1.96
2755	♀	38.8	44.5	3	2.23

Group 3: Mean weight 40.8 ± 6.4 kg, V/d = 2.74 ± 1.15 kg (S.D., n = 7).

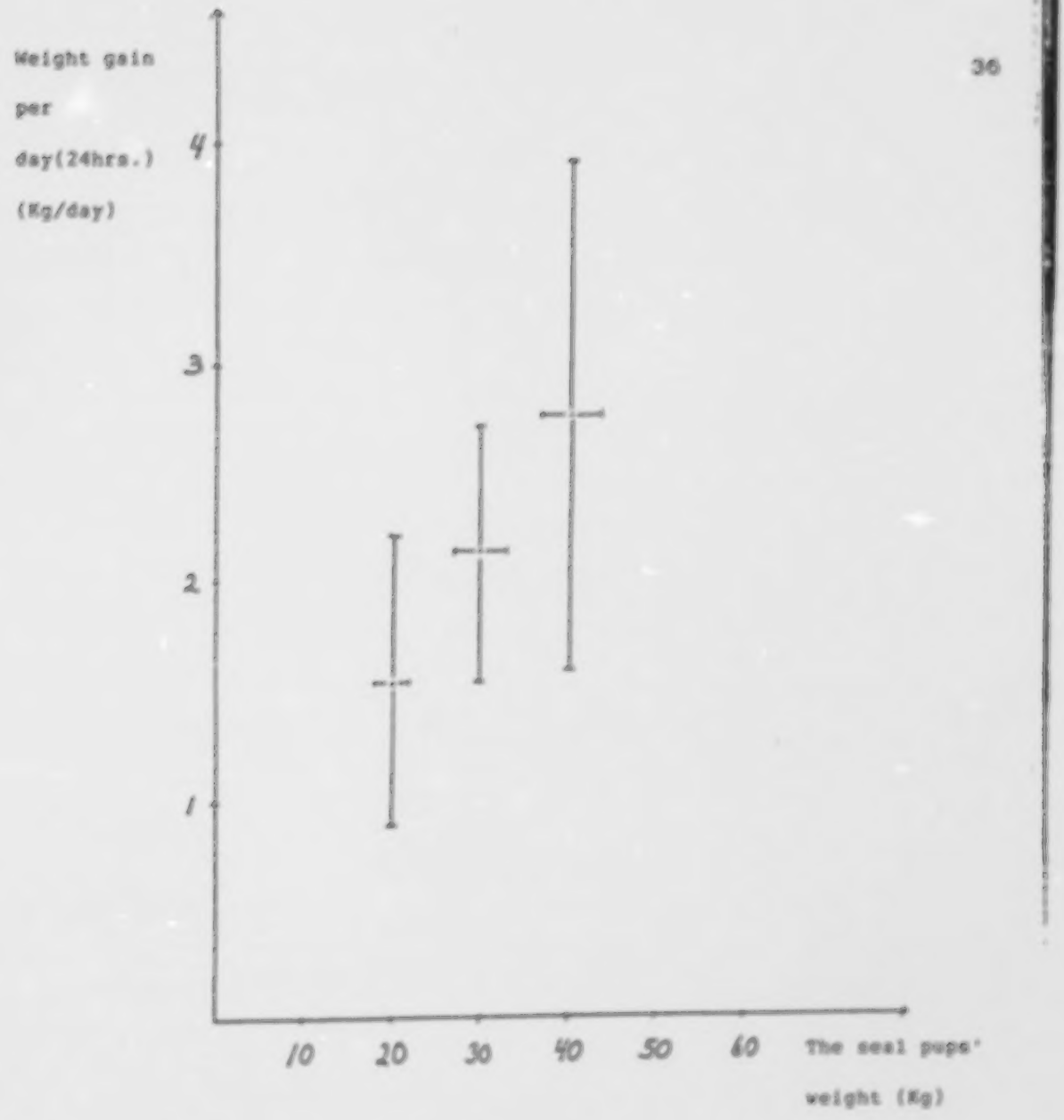


Figure 3.1.1.2 shows seal pups that are divided up into groups according to weight (along X-axis), and the average weight gain per day (24 hrs.) (along Y-axis). The values are expressed as mean value and S.D.

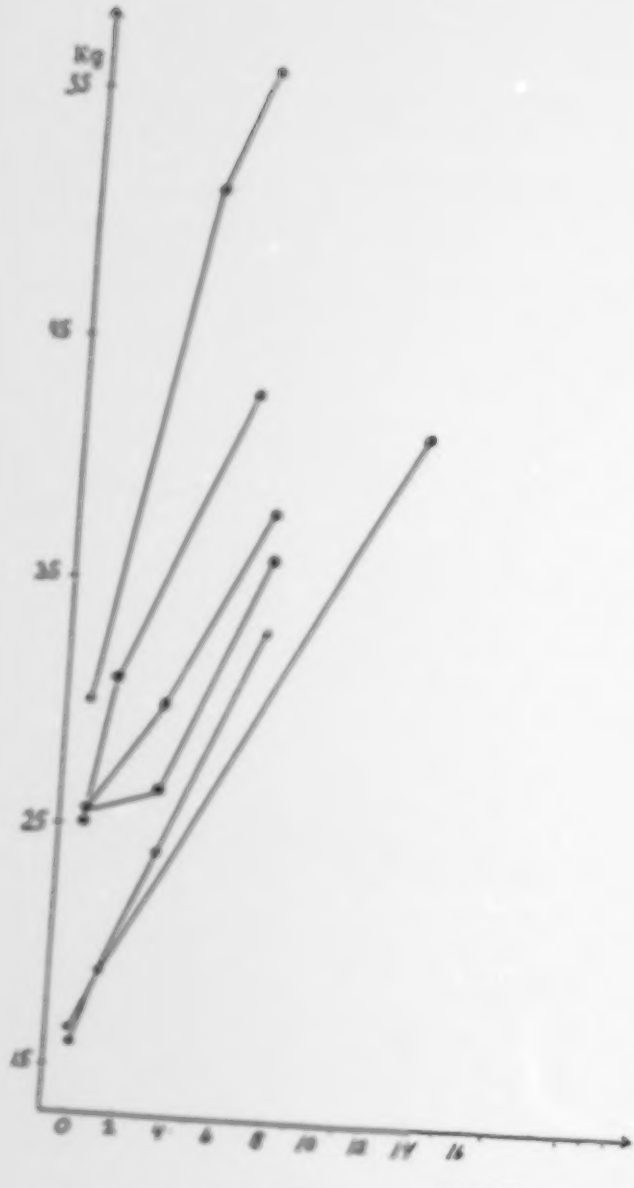


Figure 3.1.1.3 Shows the course of the weight gain in different seal pups that were weighed three times during the suckling period. Along the X-axis, the time is given in days after the first weighing, with 0 as the point in time for this. Along the Y-axis, the estimated weight is entered in kg. The lines joining the points give a possible course for the seals' weight gain curves.

Some seal pups specified in table 3.1.1.1, exhibit an unusual weight gain in that they go down during the period actually considered to be the suckling phase. Weight loss is not unusual one or two days following birth, but it is not normal further into the suckling phase. This would be the same situation as that where the seal pup was born and started the starvation period immediately. When computing weight gain during the suckling phase , such measurments would give an incorrect picture in the result. Seal 2724 showed a measurable weight loss for one day (24 hrs), but this development probably did not persist. It is therefore not included in the calculation for weight gain in group 1 that lasted from 0 to approximately five days (fig. 3.1.1.1.). Seal 2769 was more than five days old, it lacked an umbilical cord. Grey seals at this age have normally a smooth linear daily weight gain, but seal 2769 showed a daily weight loss of 0.27 kg. This is in conflict with earlier measurements (Coulson 1960). The seal was therefore not included in the weight gain calculation. Seal 2761 was weighed at intervals of a few days, and for statistical reasons these values are combined when the collective weight gain is figured out for group 1. Seal 2793 demonstrated a weight gain of 4 kg per day between the first two weighings. Later in the period, the seal was re-assessed, and had then an average weight gain of around 2 kg per day from the preceeding weighing. The latter measurement was taken over a longer interval and there is probably less uncertainty about the weight than when there is only one day (24hrs.) between weighings. The seal pups mentioned up to this point belong to group 1.

In group two, there are two seal pups that were weighed at intervals of 13 and 15 days respectively. Both weighed over 40 kg at the last weighing, and judged from a linear weight gain in the suckling period and a birth weight of about 17 kg, these seals have a suckling period of approximately 30 days. This does not agree with the previously indicated suckling periods of 14 to 21 days (p.4). Seal 2711 and seal 2734 are in consequence not included in the calculation for group 2.

WEIGHT LOSS:

The period from 6 Oct. to 13 Oct. 1979 showed mostly measurements of seal pups with weight gain. Weight loss (starvation period) was, however, also registered, and in order to obtain further information concerning weight loss in seal pups, a new round of weighing was carried out 11 days later. On 24 and 25 October, five more seal pups were noted to have weight loss in addition to the seven from the first weighing period. These seal pups are entered in table 3.1.1.2. The seals weighed during the period of fasting were measured from an average maximum weight of 41.2 kg to an average minimum weight of 35.1 kg (S.D. about 10 kg, n=8). It appeared that some of the seal pups had nursed during the time that should have been reserved for the starvation period, for which reason not more than eight were included in the calculation. In addition, some of the seven seal pups from the first weighing period were really in the suckling phase.

Weight determinations of seal pups during the starvation period give a fairly reliable weight when the suckling period is

finished. In all likelihood, the seal pups have starved for several days at the point in time when the average maximum weight was recorded. That means that the weight of the seal pups at the conclusion of the suckling period lies somewhere between 41.2 and 50 kg.

In calculating weight loss in the seals during the starvation period, one must realize that reliable observations were not made on them when the suckling period was over. This implies that the first part of the fasting period might have been, in actual fact, a period with continued nursing. The weight loss in such cases will be too small in relation to what it really ought to be. Seal 2725 had milk residues around its mouth at the time of the upper recorded weight. The weight loss for seal 2757 is half that reported earlier (Coulson 1960, Mansfield 1977), whilst at the same time the interval between the weighings during the fasting period is long. Nursing may have occurred during the first portion of the fasting period. Based on this, seal 2725 and seal 2757 were not included in the computation of diurnal weight loss incurred by the grey seal pups during the starvation period.

TABLE 3.1.1.2. WEIGHT LOSS IN GREY SEAL PUPS DURING THE PERIOD 6 OCTOBER - 25 OCTOBER, 1979, IN THE HALTEN-FROAN SECTOR.

The table shows the seal pups' no. and sex, upper and lower recorded weight in kg, number of starvation days (the interval between the weighings) and the diurnal weight loss in kg. UW = upper recorded weight, LW = lower recorded weight, StD = starvation days, and WL/D = daily weight loss.

No. D..	UW	LW	StD	WL/D
2701 ♀	56.0	45.0	12	0.92
2706 ♂	48.0	45.0	7	0.50
2714 ♀	29.6	28.0	3	0.53
"	28.0	26.0	4	0.50
2725 ♂	61.0	58.0	7	0.43
2743 ♂	44.8	37.0	17	0.46
2747 ♀	32.0	28.0	6	0.67
2756 ♀	28.0	21.5	16	0.41
2757 ♂	41.2	37.0	17	0.25
2762 ♀	44.0	34.0	12	0.83
2786 ♀	46.8	44.5	3	0.77

Average upper weight 41.2 ± 10.1 kg
Average lower weight 35.1 ± 9.3 kg
Daily weight loss 0.63 ± 0.19 kg, n = 8.

3.1.2. WEIGHT, LENGTH AND CIRCUMFERENCE FROM THE VEGA SECTOR AND THE BERGEN AQUARIUM.

The initial attempts to weigh grey seal pups during the suckling period were carried out in the Vega sector, during the second half of October 1978. Unfortunately, the weather at that time was bad, so that there are relatively few data from this sector. Table 3.1.2.1. shows the weight gain from 17 to 24 October. The results demonstrate that daily weight gain varies markedly. Two of the seals gained about three kg per day, while two other gained 0.7 and 1.5 kg per day. In the case of seal 598, that gained 0.7 kg per day, the figure is doubtful, because the mother was accidently shot for sampling due to a misunderstanding. The starvation period came therefore too early. Seal 596 has achieved a weight of close to 60 kg, and the nursing period is practically over. With a birth weight of around 17 kg, it would have taken 27 days for seal 596 to reach a weight of 58 kg. This is a week longer than the normal suckling period (Coulson 1960, Mansfield 1977). Whether the weight gain for seal 596 between the two last weighings in the wild state is due to nursing or whether it has eaten other things is uncertain. The most reliable measure of weight gain in the Vega sector is thus the measurements done on seal pups 566 and 600 during the suckling period (table 3.1.2.1).

Recording of gain in circumference and length in relation to weight gain during the suckling period was carried out in the Vega

sector and in the Bergen aquarium. The results are graphed in figure 3.1.2.1. In Coulson's work (1960), increase in length and circumference both produced a linear graph with respect to weight gain. This was done similarly in this study.

Table 3.1.2.1. Weight gain in grey seal pups in the Vega sector in Autumn 1978 during the suckling period. W_1 and W_2 represent weights at the first and second weighing in kg. D is the number of suckling days between the weighings, and V/D is the diurnal weight gain during the suckling period in kg. The seal pups are specified by number and sex.

Seal No.	W_1	W_2	D	V/D
566 ♀	27.6	48.7	7	3.0
596 ♀	56.3	57.8	4	1.5
"	57.8	59.8	3	0.7
598 ♂	25.1	27.8	4	0.7
"	27.8	24.8	3	-1.0
600 ♂	38.6	44.3	2	2.9

Average weight gain is 2.0 ± 1.1 kg (S.D., n=4)

The values recorded for seal 596 and seal 598 are however questionable. This implies that the diurnal weight gain in this sector is probably closer to three kg.

The equation for increase in length in cm in relation to weight gain i kg is:

$Y = 90.2 + 0.45\ X$, $R^2 = 0.82$, the 95% confidence interval for b = 0.45 ± 0.22.

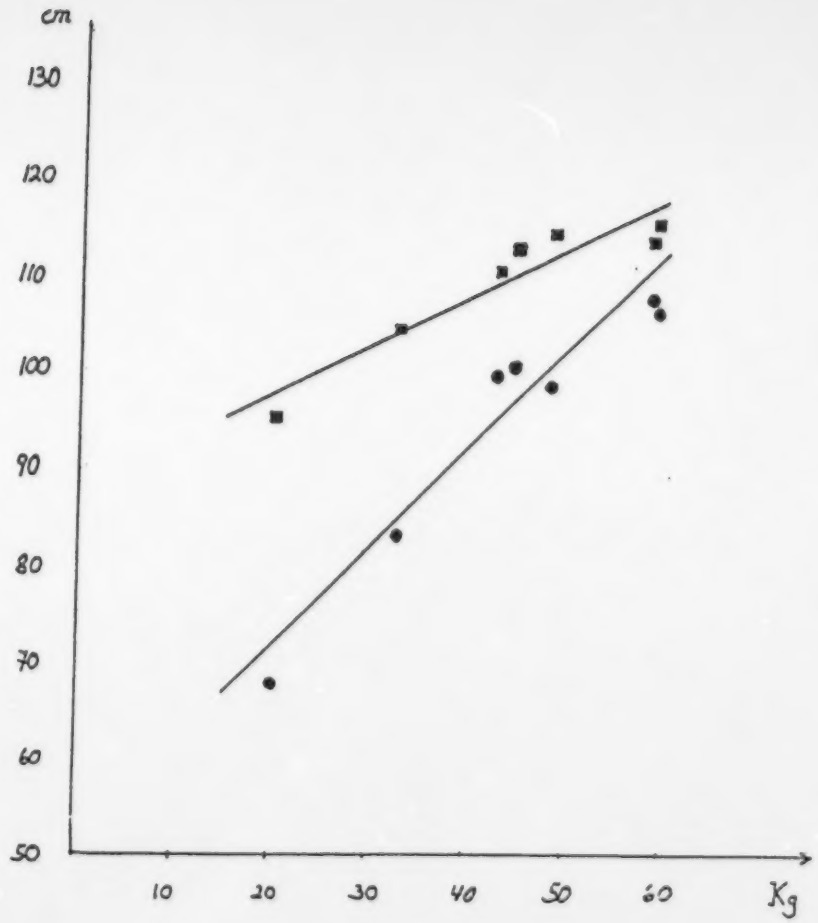
The equation for increase in circumference in cm in relation to weight gain is:

$Y = 52.2 + 0.97\ X$, $R^2 = 0.93$, the 95% confidence interval for b = 0.97 ± 0.85.

Increase in length and circumference in cm in relation to age was studied in the seal pup that was born in the Bergen aquarium in January 1980. The results are plotted in figure 3.1.2.2. Calculating with regression analysis, the equations are :

$Y_1 = 95.9 + 1.3\ X$, $R^2 = 0.97$, the 95% confidence interval for b = 1.3 ± 0.1. Y_1 is the length in cm from snout to tail (figure 2.3). X is age in days.

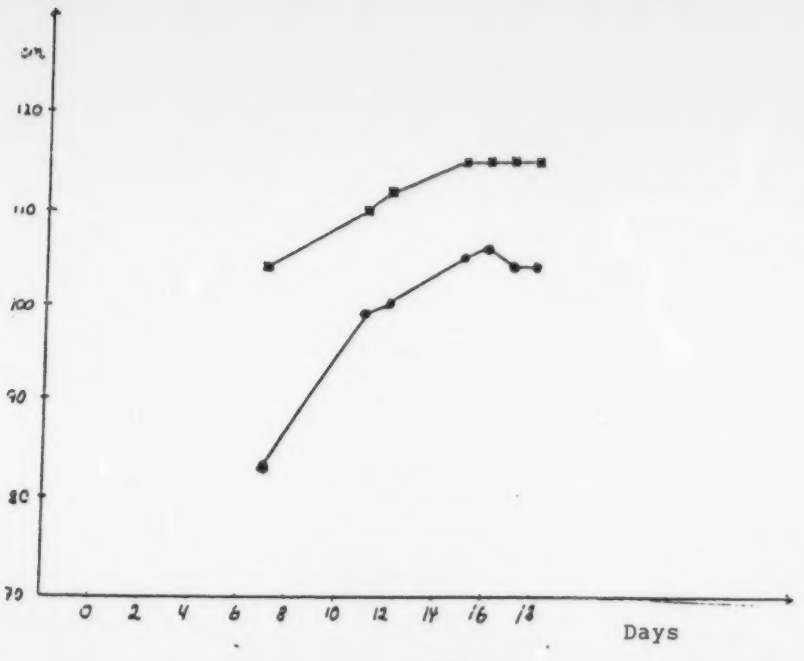
Y_0 71.4 + 2.3 X, $R^2 = 0.97$, the 95% confidence interval for b = 2.3 ± 0.2.



● Increase in circumference during the suckling period in relation to weight

■ Increase in length during the suckling period in relation to weight

Figure 3.1.2.1. Increase in length and circumference in cm is plotted in as a function of weight. Weight is determined in kg. The equation for increase in length in relation to weight gain is: $Y_1 = 90.2 + 0.45X$. The equation for increase in circumference in relation to weight is: $Y_D = 52.2 + 0.97\ X$. Every kg of weight gain in the seal pup correlates with an 0.5 cm growth in length and a 1 cm increase in circumference.



■ Increase in length during the suckling period

● Increase in circumference during the suckling period

The figure is drawn on basis of measurements from the Bergen Aquarium in Jan. 1980.

Figure 3.1.2.2. Shows increase in length and circumference in cm in relation to age in the grey seal pup born in Bergen in January, 1980. The equation for increase in length during the suckling period is: $Y_1 = 95.9 + 1.3\ X$. X represents age in days. The equation for increase in circumference during the suckling period is:

$Y_D = 71.4 + 2.3\ X.$

After 16 days, suckling was terminated, and the starvation period commenced. The figure shows that the circumference decreased sharply on the first day of the starvation period.

Measurements were also taken during the suckling period on two other grey seal pups in captivity. These measurements are derived from the Bergen aquarium, and were performed during January 1980 and January 1981 (M. Bronndal, personal communication). The seal pup from 1980 gained 2.5 kg in weight per day , while the seal pup from 1981 gained 2 kg per day. The results from these measurements are depicted in figure 3.1.2.3. From the figure, it is apparent that the weight gain in relation to age is approximately a straight line. The seal pup from 1980 was also followed up with weight measurement for the first two days of the fasting period. There is a well-defined weight loss of about three kg on the first day of the starvation period. This is also depicted in figure 3.1.2.3.

Attempts were also made to weigh the grey seal pup before and after suckling. The 1980 results are entered in table 3.1.2.2. When the seal pup was five days old, it had a series of short, frequent suckling episodes, lasting from five to ten minutes. There were two - three minutes between the sucklings. Later in the suckling period, suckling took place three times a day (i.e. per 24 hours) (I. Sangholt, personal communication). The measurements showed that the seal pup drank about 1 hg per minute during the suckling periods. Due to the fact that the seal pup did not suckle throughout the period, suckling time and the period concerned do not always agree. By assuming that the seal pup drank as much milk per minute at 5 - 6 days old as when it was 8 - 12 days old, one can estimate the amount of milk the seal pup drinks in the course of a twenty four hour day.

Suckling time from five days to six days is 46 minutes.

According to information from the guards in the Bergen aquarium there was no suckling in the period indicated by pause in table 3.1.2.2. The amount of milk drunk by the seal pup is equivalent to 4.4 ± 0.9 kg during this period (the calculation was performed on the basis of suckling time).

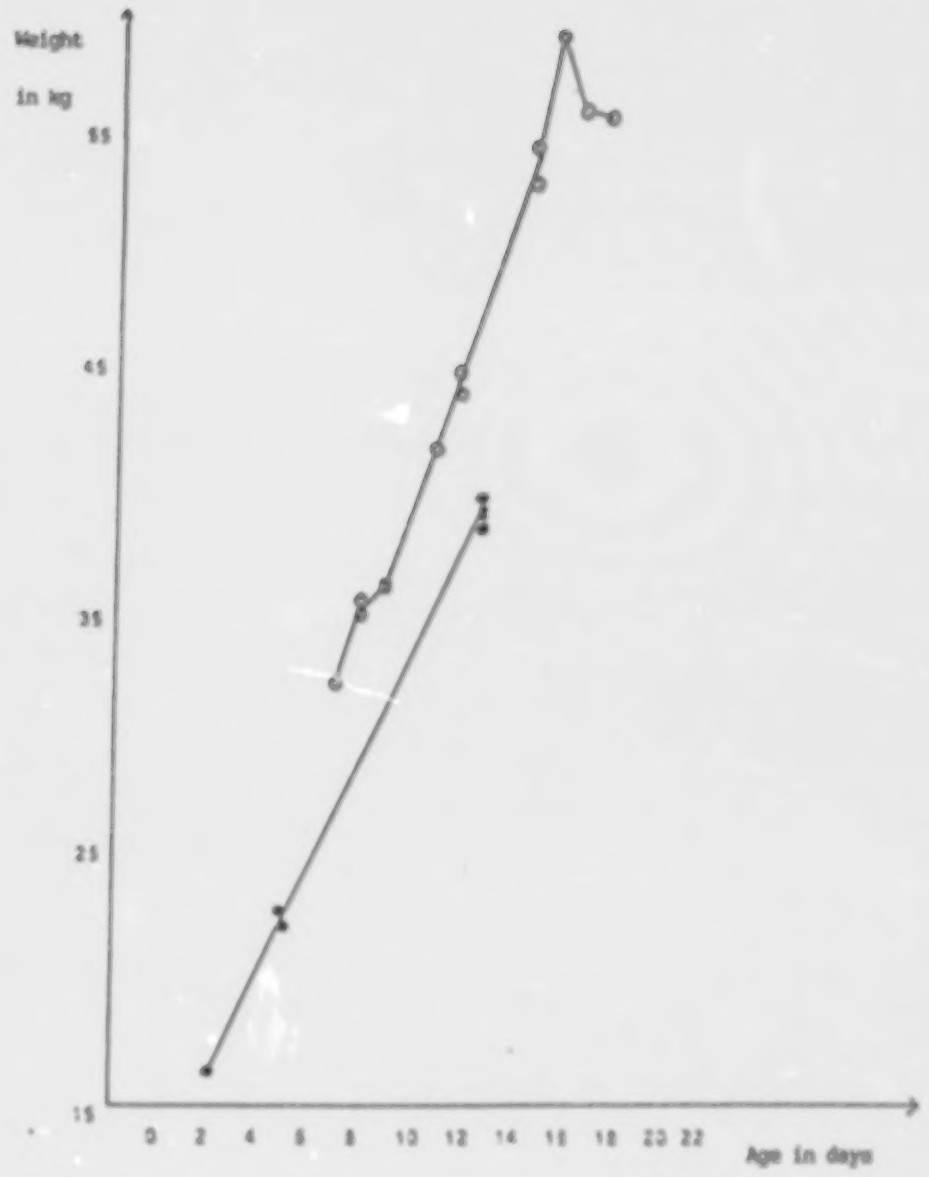


Figure 3.1.2.3. Shows the weight gain during the suckling period in two grey seal pups in captivity in the Bergen Aquarium. The circles give the determinations on the grey seal pup from January, 1980, the solid circles give the determinations on the grey seal pup from January, 1981. It is apparent from the figure that the weightgain curves during the suckling period are approximately straight-lined.

Table 3.1.2.2. shows measurements taken of suckling time and amount of milk supplied from the grey seal mother to a grey seal pup. The measurements were taken in the Bergen aquarium in January 1980. In the table, the seal pup's age in days, the suckling period, weight before and after suckling (WBS and WAS) are recorded. ST is the suckling time in minutes. Time means time of day.

Age In Days	Time	ST Minutes	WBS Kg	WAS Kg
5	1430-1436	6		
	1730-1740	10		
	1930-1937	7		
	pause			
6	0407-0412	5		
	1010-1017	7		
	1225-1236	11		
	1630-1638	8		
7	1650-1659	9		
	2203-2210	7		
8	0320-0328	8	35.2	35.6
9	1900	-		
	2050		36.4	
	2235-2243	7.5	36.4	37.3

11	1515	-		
	1640-1930	9	41.9	42.8
12	1400	-		
	1548		44.2	
	1650-1710	9	44.2	45.0

Weight gain per minute in kg : 0.96 ± 0.19 (S.D., n=4).

By making an assumption as to when during the day the seal pup nurses, and the suckling time during the different periods, when it is from six to eight days old, the suckling time comes to 46 minutes over a 24 hour day. Amount of milk provided remains the same at 4.4 ± 0.9 kg.

At the end of the suckling period the seal pup drank 1.5 kg of milk during a nursing episode. This is equivalent to 4.5 kg of milk per day (i.e. 24 hours) provided that the seal pup drank as much during the second two periods as it had per day. The suckling period of the seal pups in the Bergen aquarium was: Seal born 1980, 16 days; seal born 1981, 15 days (M. Brondal, personal communcation).

Weight Loss

On 24 October, three seal pups, no. 566, 596 and an unnumbered seal were caught, weighed and confined in comfortable, dry quarters. For the two largest pups, who had also been weighed in the free state during the suckling period, a starvation period was normal, but even the smallest (unnumbered) seal pup managed well and showed no outward evidence of diminshed activity in relation to physical development on capture. Fur coat changes were not noted either during the week of starvation. This pup weighed 23.5 kg on 24 October, and 21.8 kg on 31 October. This represents a weight loss of 0.24 kg per day.

The percentage weight loss for the unnumbered seal pup, no. 566 and no. 596 is respectively 7.2%, 12.9% and 17.6%. Whether heavy seal pups at the start of the fasting period lose most weight on a percentage basis is not discussed in the literature, but these three results suggest this.

On 1 November, seal 566 and seal 596 were transferred to the

seal laboratory at Blindern. Here the seals could be on dry land or in water, as desired. They spent most of the day in the water, even at the end of the starvation period. The weighings of seal 566 and seal 596 are depicted in figure 3.1.2.4.

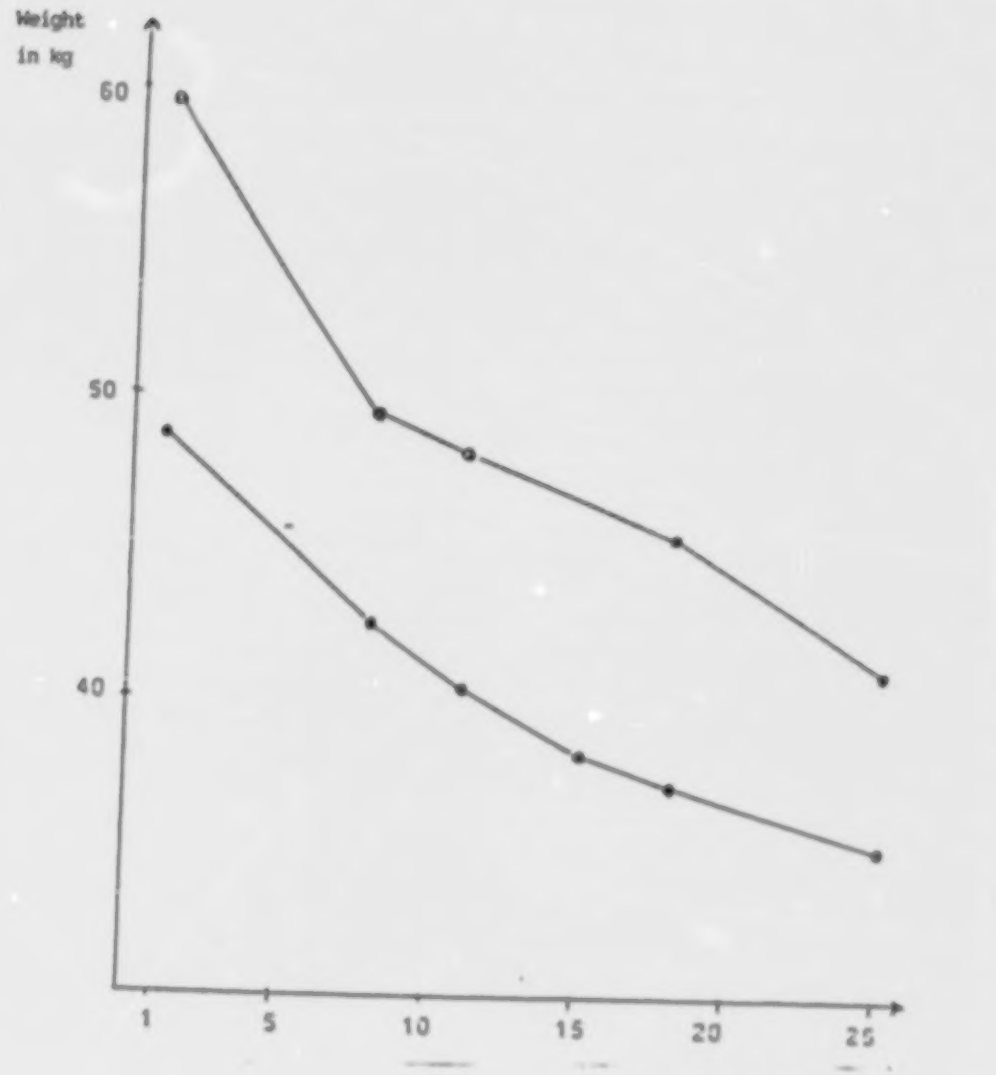


Figure 3.1.2.4. Shows seal 566 and 596 during starvation period. Seal 566 has an initial weight of 48.7 kg. Seal 596 's at the startof the starvation period is 59.8 kg. The weight loss at the beginning of the period is greater than the weight loss of the seal pups after the starvation period has lasted for more than a week. The equations that describe the weight loss during the starvation period in seal no. 566 and seal no. 596 are:

$Y = 48.7\, e^{-0.0136}$, $R^2 = 0.97$

$Y = 59.4\, e^{-0.0157}$, $R^2 = 0.94$

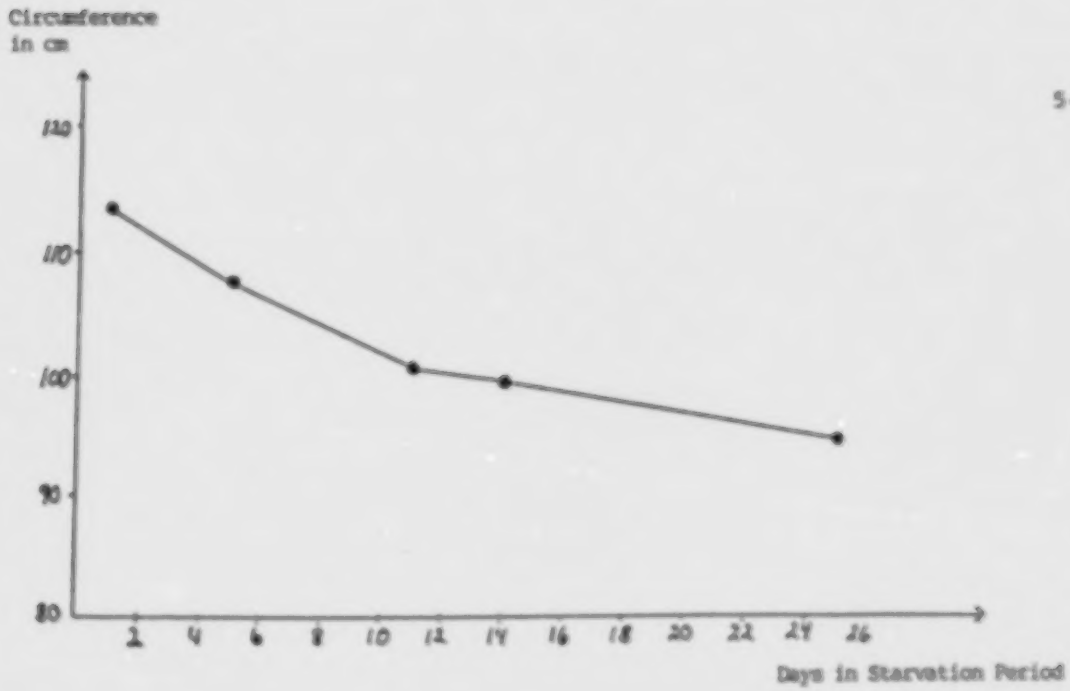


Figure 3.1.2.5. Shows the circumference of seal no. 566 during the starvation period. The circumference diminishes most during the first part of the starvation period. For mathematical reasons, the first measurement day starts with X = 1. The equation for this seal pup's circumference during the starvation period is: $Y = 114.8 - 5.81\ln x$, $R^2 = 0.97$

3.2. METABOLISM MEASUREMENTS USING BREATHING HOLE TECHNIQUE.

The metabolism of four grey seal pups was studied. Seal 596 was 8 months old, the other three 20 months when the experiments started. Seal 1, 2 and 596 were females and seal 3 was a male. The measurements were taken while the seal pups were at rest and in activity respectively. The water temperature was varied during the experiments. The seal pups' oxygen uptake was measured during periods at least ten minutes long. All the periods in an experimental series were included in the calculations, provided that nothing abnormal occurred in the course of the period. The experimental periods were divided into active periods and rest periods.

The results of the metabolic studies are given in table 3.2.1. To allow for different weights among the seal pups, the oxygen uptake was divided by the seal's body weight to the power of 0.75 (Kleiber 1975). During activity, this was between 2 and 3 L per hour, while the oxygen uptake at rest was half as great (Figure 3.2.1 and 3.2.2, table 3.2.2.).

In experiments where the seal pups were active, the swimming speed was around 1 - 1.5 metres per second. In the case of one of the experiments, seal no. 2 was in the tank while the water temperature changed. The temperature rose from 5.5 °C to 10-12 °C. The seal swam noticeably more slowly after the water temperature exceeded 10-12 °C. The water temperature increased up to 23 °C, but there was no perceptible reduction in swimming speed between 10-23 °C.

Unfortunately, it was not practically feasible to record the swimming speed at the same time as the other components of the experiments.

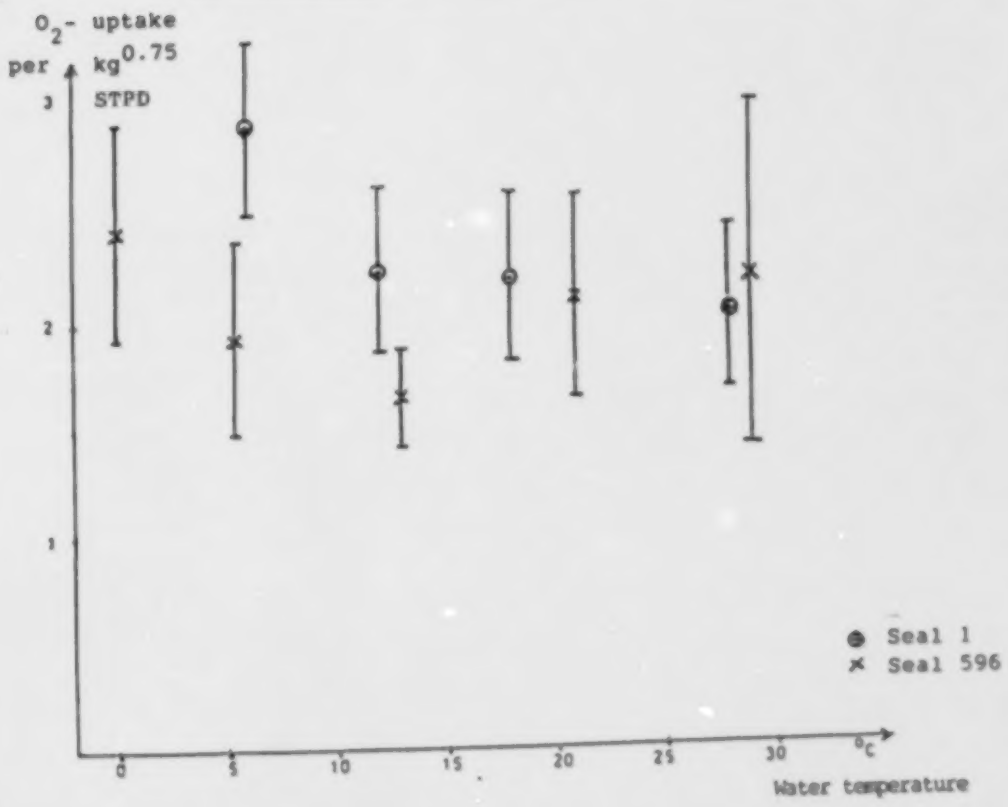


Figure 3.2.1. Metabolic studies using lean and normal grey seal pup (x) during activity.

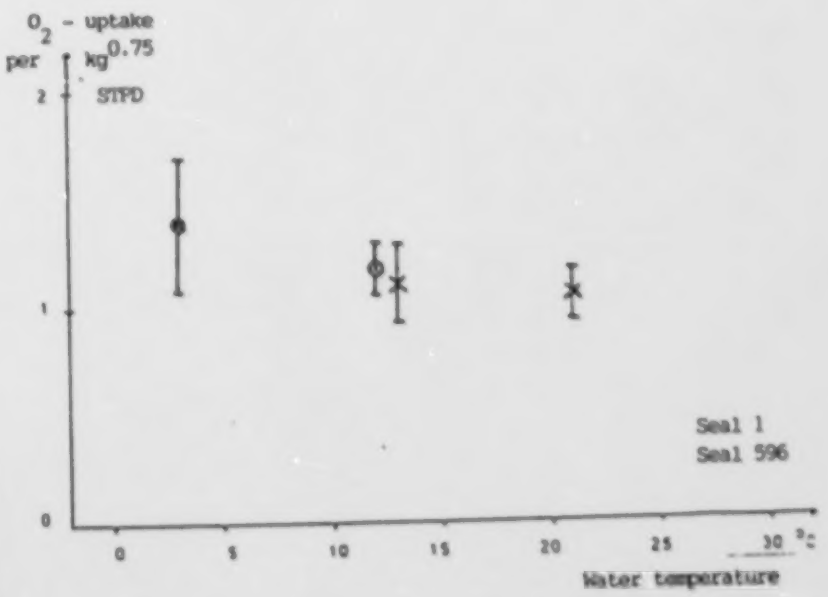


Figure 3.2.2. Metabolic studies using lean and normal grey seal pup (x) at rest.

Table 3.2.1 Metabolic Studies.

The oxygen uptake per hour with standard pressure, 0 °C and dry gas, is given by O_2 per hour STPD. The seals' computed energy utilization is given in Kcal per day (24 hours) and watts. The water temperature in °C is given by Wt. Number of measuring periods is denoted by n. The respiratory coefficient is given by RQ. The seals are denoted by number and sex.

O_2 per hour	Kcal per day (24 hrs)	Watt	Wt	n	RQ
Seal No. 596 ♀					
37.0 ± 10.6	4200 ± 1200	202 ± 58	5.5	43	0.75 ± 0.07
31.8 ± 4.2	3600 ± 500	174 ± 23	13.0	24	0.72 ± 0.06
21.2 ± 3.6	2400 ± 400	116 ± 20	13.0	4	0.69 ± 0.05
40.4 ± 8.6	4600 ± 1000	221 ± 47	21.0	15	0.70 ± 0.06
20.3 ± 2.5	2300 ± 300	111 ± 14	21.0	7	
41.8 ± 15.0	4700 ± 1700	228 ± 82	29.0	15	0.76 ± 0.04
48.9 ± 9.8	5500 ± 1100	267 ± 52	0.0	13	0.77 ± 0.05
Seal No. 1 ♀					
25.8 ± 5.7	2900 ± 600	141 ± 31	1.5	14	0.72 ± 0.03
47.3 ± 6.4	5300 ± 700	258 ± 35	5.5	29	0.73 ± 0.02
36.6 ± 6.1	4100 ± 700	200 ± 33	12.5	29	0.73 ± 0.02
19.3 ± 2.0	2200 ± 200	105 ± 11	12.5	8	0.71 ± 0.04
40.8 ± 7.0	4600 ± 800	223 ± 38	18.0	19	0.76 ± 0.05
37.7 ± 5.0	4300 ± 600	206 ± 27	28.0	9	0.73 ± 0.06
Seal No. 2 ♀					
49.0 ± 4.4	5500 ± 500	267 ± 24	5.5	9	0.69 ± 0.02
44.6 ± 3.8	5000 ± 400	244 ± 21	23.0	7	0.73 ± 0.05
Seal No. 3 ♂					
57.6 ± 5.8	6500 ± 700	315 ± 32	5.5	7	0.70 ± 0.04
54.3	6100	295	24.0	1	0.71
57.7	6500	315	24.0	1	0.72
44.2 ± 6.4	5000 ± 700	242 ± 35	16.0	5	0.73 ± 0.03

RQ for Seal 596 in all single periods (n = 121) = 0.73 ± 0.06
RQ for seal 1 in all single periods (n = 108) = 0.73 ± 0.03

Table 3.2.2 Metabolic Measurements during activity. A comparison of seal 596 and seal 1 based on oxygen uptake in L per hour per kg body weight to the power of 0.75. The table gives details of water temperature, blubber thickness and significance level. Two-tailed t-test is utilized in the comparison. The water temperature (Wt), is measured in °C, the blubber thickness is measured in cm.

O_2 pr. $kg^{0.75}$ STPD		Blubber thickness		Wt	Difference Seal 1 & 596
Seal 1	Seal 596	Seal 1	Seal 596		
-	2.2 ± 0.9		3.8	0	p -
2.9 ± 0.4	1.9 ± 0.5	1.5	3.0	5.5	$p < 0.05$
2.2 ± 0.4	1.7 ± 0.2	1.5	3.0	12.5	$p < 0.05$
2.2 ± 0.4	2.1 ± 0.4	3.0	3.0	20.0	$p < 0.05$
2.0 ± 0.4	2.2 ± 0.8	1.5	3.0	29.0	$p < 0.05$

Table 3.2.3 Shows the oxygen uptake per kg body weight to the power of 0.75 in L per hour STPD for seal 2 and seal 3. Blubber thickness and water temperature are given. The blubber thickness is measured in cm, water temperature in °C

O_2 per $kg^{0.75}$ STPD		Blubber Thickness		Wt
Seal 2	Seal 3	Seal 2	Seal 3	
2.6 ± 0.2	2.7 ± 0.3	1.5	1.5	5.5
2.6 ± 0.2	2.7 ± 0.1	1.5	1.5	23.5
	2.1 ± 0.3		1.5	16.0

The experiments were carried out over a major period of time, during which the morphology of the experimental animals altered. The seals put on weight as autumn approached, this applying most in the case of the three oldest seals, but even seal 596 gained weight. The seals' blubber thickness, together with O_2 uptake per hour per kg body weight to the power of 0.75 is given in table 3.2.2 and 3.2.3. The extent to which seal 1 and seal 596 have different oxygen uptakes is also indicated in table 3.2.2. One-way grouped variation analysis of seal 1 and seal 596 shows that the oxygen uptakes per $kg^{0.75}$ were different at the water temperatures at which they were measured ($p < 0.05$).

The respiratory coefficient, RQ, varies in the experiments from 0.69 to 0.79. In many measurements, the median value for RQ lies at 0.73 in both seal 1 and seal 596 (table 3.2.1).

No significant difference in rest metabolism was shown between seal 1 and 596 at the water temperatures at which this was measured ($p < 0.05$; this was also true when the one-tailed t-test was applied). All measurements of oxygen uptake are based on standard pressure, 0°C and dry gas.

Metabolic measurements during activity showed that seal 1 had a higher metabolism than seal 596 at water temperatures of 5-13 °C. At temperatures around 20 °C in water, the metabolism was similar, but at temperatures approaching 30 °C, the energy consumption of seal 1 was apparently lower than the energy consumption of seal 596. This was, however, not statistically significant.

Energy consumption per day (24 hours) is computed on the

basis of the metabolic measurements. When RQ is at the level found, oxygen consumption of 1 L is equivalent to 4.7 Kcal by combustion (Kleiber 1975).

In the case of seal 596, which most resembled seal pups following the suckling period with respect to blubber thickness, the energy consumption was 4200 Kcal per day (24 hours) or 200 W at water temperatures of 5.5 °C. Corresponding computations were also done in the case of the other seals that were studied (table 3.2.1).

DISCUSSION

The Shape of the Weight Gain Graph:

Mammals give sigmoid weight gain graphs (figure 4.1 and 4.2). If one imagines a sigmoid growth curve in which time is expressed per 100 days, and magnify the graph along the X-axis by using one day (24 hours) as the time segment, it is not certain that the shorter period will appear as a sigmoid-shaped graph.

Thus grey seal pups that appear to have a linear weight gain, do not necessarily need to represent an exception from a more general weight gain curve. Weight gain in grey seals, over a longer period, is not thought to be essentially different from the weight gain shown in figure 4.1 and 4.2 (figure 4.3).

For other marine mammals, it has been shown that increase in length is linear, while weight increases exponentially with time (figure 4.4). In general, the post natal weight gain curve for mammals has a shape described by

$Y = a \cdot e^{bx}$

where Y is weight in kg, a is birth weight and x is measured time (Balinsky 1975).

In the present study, it appeared, on doing regression analysis on weight and age for those animals that were age-determined on the basis of the given criteria (table 2.1), that the weight gain curve for grey seal pups in the suckling period was linear with respect to time (24 hour days). The determination coefficient $R^2 = 0.97$ for a linear graph, while $R^2 = 0.96$ for an exponential curve.

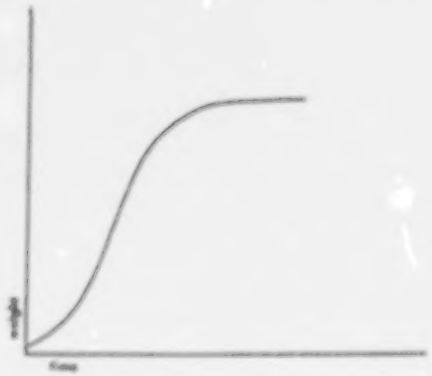


Figure 4.1 Ideal weight in mammals (Robertson, 1908, quoted by Ballinsky 1975)

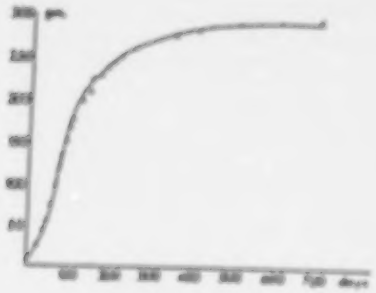


Figure 4.2 Postnatal growth in in the white rat (Donaldson et al. 1925, cited by Ballinsky 1975)

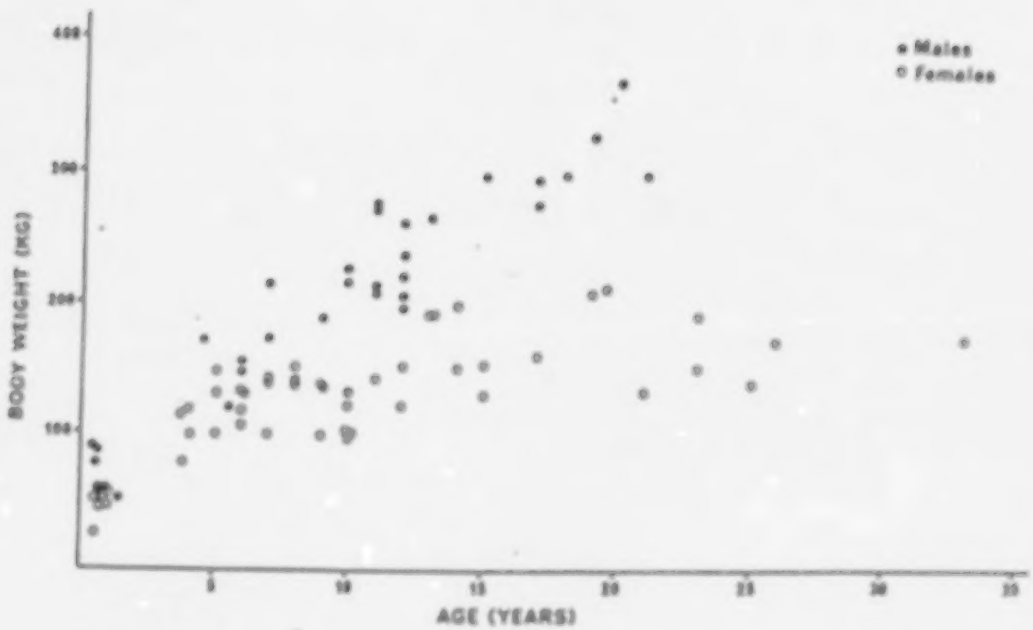


Figure 4.3 Weight gain in the grey seal (Mansfield 1977)

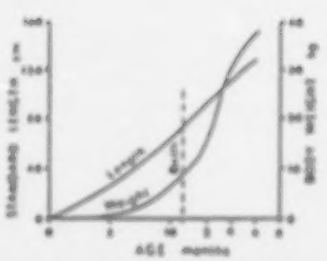


Figure 4.4
Growth in porpoises
(Harrison 1972)

of *P. phocaena* (common porpoise) from conception to six months of age.

The difference is small, but measurements in Bergen favour linearity in weight gain during the suckling period. The same can be said about free-living seal pups that are weighed more than twice in the Halten-Froan sector. In earlier studies, diurnal weight gain was considered to be linear (Stewart and Lavigne 1980, Coulson 1960).

The diurnal weight gain in grey seal pups in the 20, 30 and 40 kg weight class, exhibits, however, a different diurnal weight gain (figure 3.1.1.2). This could have been explained by an exponentially shaped curve, but there is no evidence to suggest that seal pups in these two higher weight groups have had a lower diurnal weight gain earlier in the suckling period. Observations in the present study and in the work referred to (Stewart and Lavigne 1980, Coulson 1960), indicates that a seal pup's diurnal weight gain during the suckling period is constant.

Coulson (1960) found that the average diurnal weight gain had a tendency to drop as one got further into the birthing period. He divided the 60 day long period into three. The first part was October, the second part through the middle of November and the third part from 15 November. In the article, he writes that "overpopulation" during the birthing period and the topographical circumstances were thought to be the reason behind a lower weight gain in grey seal pups that were born later in the period compared with those that were born at the beginning. If this is correct, one should expect an average rise in diurnal gain during the suckling period when the mothers' density becomes gradually less as the other seals

disappear. This is not mentioned in Coulson's study (1960).

In the Halten-Froan sector, the density of birthing seal mothers is hardly too great. Neither was it observed that grey seal males possessed harems, as in the English study (Coulson 1960). In the English sectors , the females that have given birth at an unfavourable point in time, are often obliged to move far on land and cross groups of males with harems and the females' pups in order to reach their own pups. In other words, this means extra energy expenditure in order to nurse young that owing to lack of room were delivered on the summit of the islands. Pups from the highest points on the islands had, according to Coulson, an average weight gain of 1.4 kg, whilst the average was otherwise 1.8 kg per 24 hour day. The difference is not, however, statistically significant.

Possibilities of a correspondingly reduced weight gain well into the birthing period in Norwegian grey seal pups seem improbable, since none of the pups could be said to be unfavourably placed in relation to one another. Norwegian grey seal mothers avoid, moreover, having to run the gauntlet as some of their English "relations" have to do. The weighing period was short, from 6 to 25 October, with most weighings around 6 to 13 October. By dividing the seal pups into weight groups, there is little chance of the heaviest seal pups gaining more weight because they were born at an earlier point in time and in consequence obtained a more favourable place compared with the lighter seal pups that were born later.

A possible explanation for why the heaviest (oldest) seal pups have a greater weight gain during the suckling period than the

lightest (youngest), is that those seal mothers with the strongest resources give birth earlier in the birthing period, whether or not there is "overpopulation". This implies that the seal mothers that possess the least resources for producing a successful pup in English waters may, in addition, be relegated to the poorest areas.

In English studies, it appears that the diurnal weight gain may be less than Coulson (1960) found in grey seal pups during the suckling period. An article from North Rona states that newborns weighed, on average, 14.9 and 15.8 kg (females and males). The diurnal weight gain in females and males was respectively 1.3 and 1.4 kg during the suckling period that lasted 17 days. On average, 2250 pups were born here annually, with a mortality of 18% during the nursing period (Boyd and Campbell 1971). The birth weight here was somewhat higher than that Coulson (1960) stated for the Farne Islands. The studies do not say whether or not the seals were wet, but that may explain the weight difference.

Concerning mortality and disease during the nursing period in the Halten-Froan sector, one pup was recorded having died of unknown cause. Another pup that had diarrhoea, recovered, whilst infection in and around the umbilical cord was not observed. Infections via the umbilical cord to the abdominal cavity, and starvation, are the main causes of death among English grey seal pups during the suckling period (Baker et al. 1980). This can probably be attributed to a situation with seal "overpopulation", resulting in a great deal of excrement, infected soil and great risk of infection for individuals that cannot rinse themselves off. The pups' umbilical

cord is obviously vulnerable due to thin skin and small tears in connection with movement.

The average weight gain found in the present study is similar to the average weight gain noted in Canadian grey seal pups during the suckling period (Mansfield 1977). Mansfield concluded by saying that the Canadian grey seal was larger, heavier, had greater birth weight and lived a little longer than the English grey seal. The Canadian grey seal pups attained upper weight in the suckling period 4-5 days before the English grey seal pups. On the basis of the study in the Halten-Froan sector, it appears that both the suckling period and the seal pups' weight gain during the suckling period agree best with the findings for the Canadian grey seal. Birth weight in Norwegian grey seal pups also approaches that of Canadian grey seal. The duration of the suckling period is based on measurements from the Aquarium in Bergen, linearity in the weight gain curve and an upper average weight between 41.2 and 50 kg.

It is considered reasonable to assume that seal with good access to nutrition could grow faster and become larger than seal with poorer resources at their disposal. It seems also reasonable that a large seal mother is able to supply more milk than a smaller seal mother, so that the larger mother's pup could become larger and grow more quickly than the small seal mother's pup during the nursing period. The assumption here is that the pup's food intake does not limit its growth. By the very fact that weight gains of both four and five kg were measured (D 2793 and D 2701, table 3.1.1.1), the pup's

nutritional uptake is not thought to be a limiting factor in growth. Some reservation is, however in order concerning the genetic diathesis.

A comparison between the growth rate of English and Norwegian grey seal pups during the suckling period, with regard to the nutritional conditions, would be of interest. Coulson's (1960) results from the Farne Islands are used for the English seal pups.

For Norwegian and English grey seal males (pups in the suckling period), there was a significant difference in diurnal weight gain ($p < 0.05$, two-tailed t-test). The average value for the English males was 2.37 kg per day (24 hours), the value for the English grey seal males was 1.86 kg per day (24 hours). For nursing Norwegian and English grey seal females there was no significant difference ($p > 0.05$; this was also the case using the one-tailed t-test). Diurnal weight gain during the suckling period was 1.9 kg for Norwegian female pups, while the English females had an average diurnal value of 1.72 kg. Due to great variations in the material, there was no significant difference between Norwegian and English female pups average diurnal weight gain during the suckling period.

Increase in Length and Circumference during the Suckling period

In this study there are few and unreliable data pertaining to these parameters. Measurements are often difficult to take owing to the fact that the seal does not lie still. The 95% confidence interval is so great that it is not possible to say whether there is any difference between Norwegian and English grey seal pups on the

basis of the present data, either in measurements of circumference or length.

The Starvation Period

Weight Loss

At the beginning of a starvation period, water loss will be great (Gilder et al. 1967) As the fasting period continues, the diurnal weight loss is reduced (Kleiber 1975). Since the seals are not all the same age, the average figure for weight loss will probably smooth out large water losses and metabolic depression. The average diurnal weight loss was 0.6 kg for grey seal pups in the Halten-Froan sector. Average weight of the pups was from a good 40 kg and down to 35 kg during the starvation period.

In an unpublished article, it was found that a weight loss of one kg in grey seal pups of the same age and weight is equivalent to 7200 Kcal during the starvation period (Øritsland et al. unpublished). The weight loss in grey seal pups in the Halten-Froan sector constitutes 4300 ± 1600 Kcal diurnally based on this calorie equivalent. The energy equivalent is found by metabolic measurements over extended time during the starvation period and weight determinations before and after these. The weight loss and metabolism will thus tell us how much energy a loss of one kg corresponds to in Kcal.

The graphs obtained for seals 566 and 596 during the starvation period showed that they suffered a weight loss of 0.55 and 0.60 kg respectively when they weighed around 40 kg. The average

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diurnal weight loss found under natural conditions seems therefore plausible.

Standard Kleiber Metabolism

$M = 70 \cdot W^{0.75}$

M represents Kcal per day (24 hours), W is the weight of a mammal; for a 40 kg seal this is 1120 Kcal diurnally. That is to say that the seal pups in portions of the starvation period lie 3.5 - 4 times above "normal resting metabolism" (Kleiber 1975).

For seal 596, free-swimming with breathing hole technique, the caloric value was computed on the basis of oxygen consumption to be 4200 ± 1200 Kcal diurnally at a water temperature of 5.5 °C. This was found during continuous diving (swimming) interrupted by brief breathing periods. It seems odd that the metabolism of a swimming (diving) grey seal is less than the estimated metabolism of seal pups under natural conditions. The seal pups in the Halten-Froan sector do certainly have rest periods in the course of the day (personal observation).

Other factors, however, may play a roll. A free-living seal pup has greater possibilities for movement than one living in captivity. From observed activity in the Halten-Froan sector, one could not tell that the seal pups here were more active than the seal pups in the tanks at Blindern (personal observation). The seal pups in this sector are more exposed to wind, rain and sea spray than the seal pups in captivity with which they are compared. Constant sea spray may cause increased evaporative cooling in animals that lie exposed. In the water, wave movement would in all likelihood mean

that swimming would demand more energy than in a tank.

Irving (1934, 1938) suggested that seal could undertake longer dives than supposed, taking into consideration their oxygen consumption and the oxygen the animals brought with them at the beginning of the dive, by reason of the fact that the seals were able to redistribute their blood supply. Diving seals could almost be perceived as a brain-heart preparation. A depressed metabolism during quiet diving has also been proposed by others (Harrison 1968).

During the experiments, it might thus be possible that the seals have a lower metabolism than when they are on land. Harrison (1968) based his findings on a dive that lasted 18 minutes. In the present study, the duration of the surface dives varied from two to four minutes.

A heart rate corresponding to that noted in diving seal is also found in seal on land (Påsche and Krog 1980). It appears therefore reasonable to presume that the metabolic values found during activity in water do not differ substantially from those values to be anticipated on land. The oxygen uptake found during diving in the present study is, moreover, so high that it seems unlikely that the metabolism could be depressed.

A diurnal calorie equivalent of 7200 Kcal indicates that the bulk of the seal's combustion is fat. The energy equivalent of fat, water excluded, is 9.4 Kcal per kg (Pike and Brown 1975), while that for fat-free body weight is reckoned to be from 1.4 - 2.4 Kcal per kg (Gorecki 1975). Seal blubber contains approximately 10% water (Ortiz et al. 1978). Were the body to comprise the main portion of what

is combusted, a much lower energy equivalent per kg would result.

Stewart and Lavigne (1980) found that Greenland seal pups during the fasting period had a weight loss of 10% from blubber and 35% from carcass. If this is used as a base for this study, a diurnal weight loss of 0.6 kg would be equivalent to a diurnal calorie consumption of 2100 Kcal. This corresponds to 1.9 times the Kleiber level, equal to normal rest metabolism in these animals. When one takes into account the fact that the seals were observed in the sea a good part of the day, this seems too low a calorie consumption.

From a purely energetics point of view, it seems disadvantageous to burn a lot of protein. The caloric value of protein is 5.7 Kcal per g, whilst the catabolic value is 4.8 Kcal per g. This is the case by reason of the fact that mammals do not oxidize nitrogen compounds completely, but excrete them as urea (Kleiber 1975).

In the free state, the seal pup has to capture prey animals following the starvation period. Therefore it would hardly seem logical that right from the start it would consume the very tissue that would give the seal pup the means to capture its prey.

The average RQ value in metabolic studies was 0.73. This corresponds to about 80% combustion of fats and 20% combustion of proteins (Kleiber 1975). The duration of the experiments was circa 20 hours for each seal. Possible discharge or uptake of carbon dioxide ought not to be any problem.

RQ-measurements in adult Greenland seal lie between 0.70 and 0.75 (Øritsland and Ronald 1975). Similar RQ-values were obtained

in the case of Greenland seal pups (Hart and Irving 1957).

In two articles on elephant seal (Mirounga leonina) it is written that combustion of fat is the usual response during a starvation period. This hold true for both adult individuals and pups. The pups can also be in water balance despite the fact that they combust only fat (Keith et al. 1980, Ortiz et al. 1978). Brodie and Påsche (1980) write in their article that during starvation the seal burns internal fat resources, if available, after that the outer insulating blubber down to a critical value. Following this begins combustion of muscle tissue. Finally, the remaining blubber will then be consumed. This agrees with the caloric data found by Øritsland et al. (unpublished). It seems that combustion of fat at the beginning of the pup's starvation period would be reasonable in view of the articles in question. This is in contrast to what Stewart and Lavigne assert, but it may be that they have measured water loss in the carcass at the beginning of the starvation period (Gilder et al. 1967).

Stewart and Lavigne included the weight of blood along with the carcass in their weight determinations. Mansfield (1977), does not write that the same is true in his study, but judging from weights of carcass, blubber and total weight, it appears that the same holds for this study. Mansfield found that carcass and hide, including blubber, maintained a 1:1 ratio during the grey seal pup's period of starvation, whilst Stewart and Lavigne (1980) found a carcass weight loss of 35% and a hide and blubber loss of 10% in

Greenland seal pups. Mansfield's determination of age was based on observations of each seal pup; Stewart and Lavigne accurately determined the age of relatively many Greenland seal pups and calculated the age of the remaining pups on the basis of weight and the age corresponding to weight in the case of the accurately age-determined pups. Mansfield's (1977) study suggests that blubber comprises the bulk of the grey seal pups' energy turnover during the starvation period, something that the present study supports.

Metabolic Measurements

The RQ-value of the youngest seal, 596, had a greater standard deviation than the RQ-value of the oldest, seal 1, 0.06 contrasted with 0.03 respectively. This could be attributed to the elder seal's greater experience with such experiments. The average RQ-value of 0.73 was valid for both seals.

The resting metabolism found is in accordance with other studies (Irving 1969). It does not appear that varying heart rate, which grey seals can exhibit in various types of sleep, has manifested itself in the study (Ridgeway et al. 1975). Brodie and Påsche (1980) found that resting metabolism of lean grey seals was higher than in those with a normal blubber layer (Øritsland et al. unpublished quote). At the temperatures at which resting metabolism was measured, there was no difference between the lean and normal grey seal. It could be, however, that the experiments came within the thermoneutral range, such that the lean grey seal had no need to increase its metabolism in order to equilibrate deep body temperature.

The observation contrasts with what Miller and Irving (1975) wrote, that resting metabolism in the newborn common seal would have been less in comparis on with the resting metabolism of an adult common seal if fat-free body weight formed the basis for the calculation. Since the adult seal had more blubber percentwise, and this tissue had a lower metabolic rate than musculature or viscera, Kerwick (1965) states that fat and musculature have the same resting metabolism. Other studies concur (Mc Nab 1968, Øritsland personal communication). The results for seal 1 and seal 596 thus seem feasible.

During activity, metabolism can hardly be the same in blubber and other tissue. Some of the content in fat cells exists as oil, a point that must be taken into account when the metabolism per kg is worked out.

In studies of this type, there is always the possibility that experimental animals have their own idiosyncrasies. It is, for example, possible that seal 1 may exhibit a general activity greater that normally shown by seal 596. During activity, the oxygen uptake of seal 1 falls with rising water temperature, the oxygen uptake of seal 596 rises when the water temperature is more than 20 °C. This suggests that insulation influences the behavior of the seals.

Elevated metabolism with high water temperature in seal 596 could be explained by augmented pumping of blood to peripheral tissue in order to promote greater heat loss.

Seal 1 behaved strangely during a metabolic study with water at 1.5 °C, in that its activity was minimal. If this seal at the time of this experiment had too poor an insulation, it could be

that by swimming faster than it did in the equivalent experiment at 5.5 °C, it would experience an increased heat loss by convection, that exceeded the muscles' augmented heat production due to swimming. In such a situation it would be able to survive longest by remaining still. It would then increase the insulating water layer in its fur coat (Frisch et al. 1974) and the temperature in the peripheral muscle tissue would probably sink somewhat in such a case (Hart and Irving 1957). Shivering or combustion of brown fat, if available, would be a valid option, but is considered somewhat speculative.

The insulation (the blubber layer) was three cm at the time of the experiment in water at 1.5 °C, whilst it was 1.5 cm when the experiment was performed in water at 5.5 °C. This favours the view that other things have affected the seal.

Brodie and Påsche (1980) based their article on rest metabolism in grey seal pups during the starvation period. The authors found that the resting metabolism in water showed a marked, progressive rise as the blubber layer (insulation) became thinner. When the blubber layer decreased from 2 to 1.5 cm, the metabolism rose by 30%.

In the study performed on seal 1 and seal 596 during activity, the oxygen uptake per kg body weight to the power of 0.75 shows that seal 1 has a metabolism about 1.5 times that of seal 596 at 5.5 °C in water. From figure 3.2.1, it is seen that the oxygen uptake of seal 1 exceeds the oxygen uptake of seal 596 when the water temperature is 15 °C or colder. The difference is greatest at the coldest water temperatures. From an energy point of view, a seal

ought to have a well insulating blubber layer.

Figure 3.2.1 suggests that the oxygen uptake during activity does not rise in linear fashion. If the seal swims in order to achieve equilibrium in its deep body temperature, this means that it must lose some of the muscles' surplus heat production with faster swimming. The first thought to occur is that of augmented blood flow through parts of the body with increased metabolic activity, such that the heat loss to water increases with stepped-up blood perfusion through, for example, the flippers. Diving seals have certainly been described as a brain-heart preparation, but the shutting-off of veins cannot be 100% effective over a prolonged period of time. The tissue would then die.

The body composition differed somewhat in seal 1 and seal 596 at the time of the experiments. A direct comparison would therefore be open to doubt. Seal 596 has more blubber than seal 1 on a percentage basis. During activity it is probable that the metabolic rate for one kg of fat tissue is lower than that for 1 kg of muscle tissue, so that seal 596 emerges as the more fortunate from an energy standpoint. Seal 596 is, however, one year younger than seal 1. That would seem to justify its having a relatively higher metabolism than seal 1. The study supports Brodie and Pâsches' assertion (1980) that a non-linear increase in feed intake is possible in growing populations of marine mammals, since a decrease in blubber layer at constant water temperature, may be equated with a constant blubber layer and a fall in water temperature.

Even though the lean seal has a higher energy consumption

than the normal eel, it ought to be mentioned that the lean eel has probably swum a longer distance than the normal eel in the same time. The body friction in water would, however, be proportional to the square root of the velocity, so that consumed energy per distance would be greater for the hyperactive eel than for the normal one.

Energy Transfer and Consumption in a Seal Mother with Pup during the Suckling Period

Amoroso and Mathews (1952) showed that a grey seal pup had a weight gain that was half that of the mother's weight loss. Mansfield (1977) found that 60% of the weight loss in the seal mother derived from blubber and 40% from carcass, in the grey seal.

By assuming that the energy consumption of the pup during the suckling period , is the same as that in the starvation period, it is possible to draw up a yardstick for the energy transfer: seal mother - pup. The following calory equivalents apply for fats, proteins and carbohydrates (Pike and Brown 1975). The values are expressed in Kcal per g. Energy = E.

Nutritional material	E	Digestible E	Metabolisable E
Fat	9.4	9.0	9,0
Protein	5.65	5.20	4.0
Carbohydrate	4.15	4.0	4.0

The caloric value of fat-free body weight is reckoned to be from 1.4 to 2.2 Kcal per kg. The energy equivalent of the seal pup carcass is estimated at 1.4 Kcal per g (Gorecki 1975). This is done because the weight of blood is included in the carcass in Mansfield's (1977) study. Mansfield knew that the pup's weight gain during the suckling period consisted of a gain of 4 - 23 kg for hide and blubber and a gain of 10 - 23 kg for carcass.

The mother's weight loss when the pup has a diurnal gain of 2.1 kg in weight is 4.2 kg diurnally. The water content of seal

blubber is 10% (Ortiz et al. 1978). The calorie equivalent of seal blubber is therefore 8.5 Kcal. per kg. In view of the fact that younger mammals have more water content in fat-free body weight than older ones, the calorie equivalent for the seal mother's carcass is put at 2.0 Kcalories per g (Haecker 1914, Armsby, 1922 in Kleiber 1975), (Øritsland 1977)

The mothers weight loss in Kcal is:

Fat	21,420 Kcal
Protein	3,360 " "
In total, this corresponds to	25,000 Kcal

The pup's energy consumption and energy uptake during the suckling period:

66% of the weight gain is in blubber, 34% of the weight gain is in carcass. Account is taken of the amount of energy that is lost through digestion of fat and protein. Carbohydrate is not included in the calculation.

The pup's energy consumption	4,300 Kcal
Storage of blubber	12,200 " "
Storage in carcass	1,100 " "
In total, this corresponds to	17,600 Kcal
Loss through digestion	600 Kcal

The grey seal milk contains small amounts of lactose, so that the pup

during the suckling period is assumed to burn a minimal amount of protein. If the fat content of milk is used as a basis to estimate how much milk the seal pup must drink to put on 2.1 kg diurnally, the smallest amount of milk it has to drink is about 3.3 kg.

This amount of milk also meets the seal pup's protein requirements. The same also applies if the calculation is based on the highest calorie equivalent for carcass.

The seal pup in Bergen (1980) gained weight amounting to 57% of the supplied amount of milk. A 60% weight gain in relation to the amount of milk supplied seems like a reasonable estimate, in view of the fact that neither the calculation based on weight studies before nor after suckling can be fully accurate. This means that the seal pup must drink 3.5 kg of milk in order to gain 2.1 kg in weight diurnally. The calorie content of 3.5 kg of milk is 19,000 Kcal.

The mother's metabolism during the suckling period is:

Food intake (estimated)	0	Kcal
Weight loss comprises	22,000	" "
Energy content of milk	19,900	" "
The mother consumes herself	5,100	Kcal

This computation must be considered to be very rough, and the quoted figures are to be taken more as a pointer indicating in which region the mother's metabolism lies rather than the precise value. In herring, such a metabolic level corresponds to 2.1 kg (Fiskets gang No. 4, 1977).

Conclusion:

Birth weight for Norwegian grey seal pups is 16.6 ± 1.3 kg. Diurnal weight gain during the suckling period, which varies from 15 to 16 days, is 2.1 ± 0.9 kg. The weight gain for Norwegian and English male grey seal pups was different during the suckling period. The Norwegian male pups gained 2.4 kg diurnally, the English males 1.9 kg diurnally. For female pups there was also a difference in weight gain during the suckling period. Norwegian female pups gained 1.9 kg diurnally, whilst the English female pups gained 1.7 kg diurnally. The difference in the males' weight gain was at the 5% significance level; however, this did not apply to weight gain in the female pups. There was no difference either in weight gain at the 5% significance level between Norwegian male and female pups during the suckling period.

The results found for Norwegian grey seals are near those obtained for Canadian grey seals, both where average weight gain during the suckling period and duration of the suckling period is concerned. Average weight gain was identical, the suckling period for Canadian grey seals was 14 to 15 days.

One of the Norwegian grey seal pups was found dead during the suckling period. Ninety pups were weighed in all, so mortality in relation to the English pups, stated to be 18%, must be characterized as low.

Weight loss in Norwegian grey seal pups during the starvation period, following the suckling period, was 0.6 ± 0.2 kg. The weight loss was greatest at the beginning, and became less over

the course of the starvation period.

Control studies, using seal pups in captivity, showed that the metabolic level of a seal with similar body composition, was approximately the same as the calculated energy consumption for free-living seal pups during the starvation period, 4300 Kcal or a little over 200W.

During metabolic studies of a lean and a normal grey seal it was shown that the lean was at a metabolic level 1.5 times higher than the normal during activity. It looked as if this could be explained by the leanest seal's poorer insulation. For both of the seals the metabolic level varied with varying water temperature while the seals were active.

The seals' resting metabolism in water, was about double that calculated for normal resting metabolism in mammals. There was no difference in the resting metabolism between the lean and the normal seal at water temperatures around 13 and 20 °C.

At water temperatures approaching 30 °C, the metabolism of the lean seal during activity was apparently lower than that of the normal one. The difference between them became less as the water temperature rose from 5 °C and upwards. The metabolism during activity was considered to exhibit a non-linear increase with declining water temperature from 13 to 0 °C.

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